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Un nouvel Acanthodactyle en Algérie : *Acanthodactylus taghitensis* n. sp. (Reptilia, Sauria, Lacertidae)

par Philippe GENIEZ et Antoine FOUCART

Résumé. — Un nouvel Acanthodactyle du groupe *scutellatus* découvert en Algérie, dans la région de Beni Abbès, est décrit sous le nom de *Acanthodactylus taghitensis*, de Taghit, localité-type. Cette espèce se caractérise surtout par la différence de taille entre les écailles dorsales et celles des flancs, par la possession de quatre supralabiales en avant de la suboculaire et par un patron de coloration particulier.

Mots-clés. — *Acanthodactylus taghitensis,* Lacertidae, systématique, Sahara, Algérie.

A new Fringe-toed Lizard from Algeria : *Acanthodactylus taghitensis* n. sp. (Reptilia, Sauria, Lacertidae)

Abstract. — A new Fringe-toed Lizard of the *scutellatus* group found in Algeria, in the Beni Abbès area, is described under the name of *Acanthodactylus taghitensis*, from Taghit, type locality. This species is especially characterized by the size difference between dorsal and lateral scales, by the possession of four supralabials in front of the subocular and by an original colour pattern.

Keywords. — *Acanthodactylus taghitensis,* Lacertidae, systematics, Sahara, Algeria.

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INTRODUCTION

Au cours d'un trajet de liaison, lors d'une mission d'étude sur le Criquet pèlerin *Schistocerca gregaria* (Forsskål, 1775) programmée par le CIRAD-PRIFAS, l'un de nous (A. F.) a prélevé, 36 km après Taghit en direction de Beni Abbès, un Acanthodactyle répondant à des caractéristiques morphologiques (écaillure, coloration) qui, lorsqu'elles sont combinées, ne permettent d'attribuer cet animal à aucune espèce du genre *Acanthodactylus* décrite jusqu'alors. Par ailleurs, un spécimen pouvant être rapporté à la même espèce a été photographié par M. GENIEZ, 5 km après Taghit en direction de Beni Abbès. L'existence de deux animaux semblables et aussi particuliers en regard des autres représentants du genre *Acanthodactylus*, provenant de deux localités éloignées de quelque 30 km, suggère fortement, malgré la faiblesse de l'échantillon, que nous avons affaire à une espèce nouvelle.

DESCRIPTION

Les deux Acanthodactyles de la région de Taghit, des femelles, appartiennent au groupe *scutellatus* (*sensu* SALVADOR, 1982 ; ARNOLD, 1983) : quatre rangées d'écailles autour des doigts, écaille suboculaire ne touchant pas la lèvre, quatrième orteil fortement pectiné, écailles ventrales disposées en séries transversales obliques, museau pointu, coloration pâle et peu contrastée. Leur coloration générale est d'un beige roussâtre pâle ou orangé clair. Le dos est parsemé de petites taches sombres (occupant chacune une à trois écailles) très espacées et grossièrement disposées en cinq rangées longitudinales (fig. 1). Ces taches sont reliées par des traits pâles qui s'estompent plus ou moins dans le tiers postérieur du dos. Les écailles labiales et la suboculaire sont uniformément pâles. La face ventrale est blanc pur. En ce qui concerne l'écaillure, on note 1 ou 2 granules insérés entre les pariétales, 1 rangée complète de granules supraciliaires, se dédoublant en arrière de la troisième supra-oculaire, 4 labiales en avant de la suboculaire, cette dernière étant en contact avec les labiales 4 et 5 (fig. 2). Les écailles dorsales et latérales sont carénées et tectiformes, celles du dos étant environ deux fois plus grandes que les latérales. Le passage des écailles du dos aux latérales s'effectue brusquement (fig. 3). On compte 30 séries obliques transversales d'écailles ventrales disposées en 14 rangées à mi-corps.

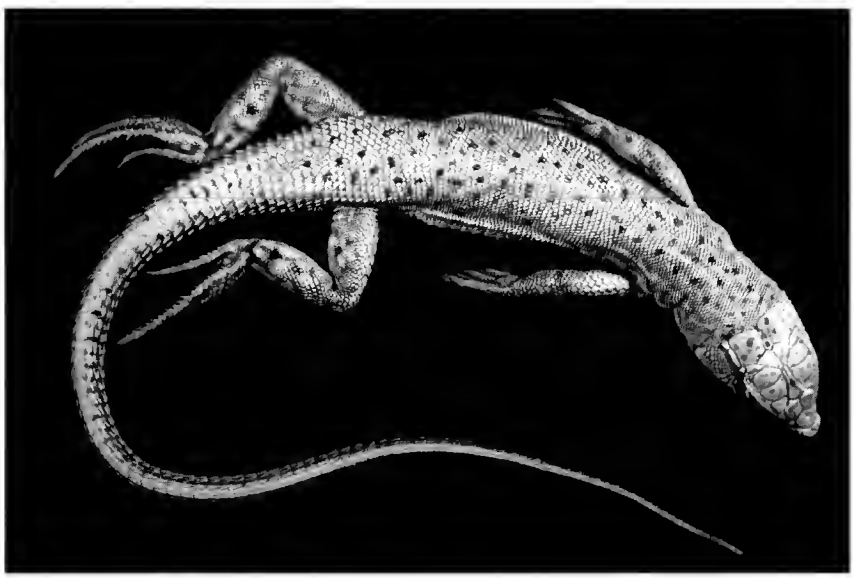

FIG. 1. — Vue dorsale de l'holotype d'*Acanthodactylus taghitensis* n. sp.
Dorsal view of the holotype Acanthodactylus taghitensis *n. sp.*

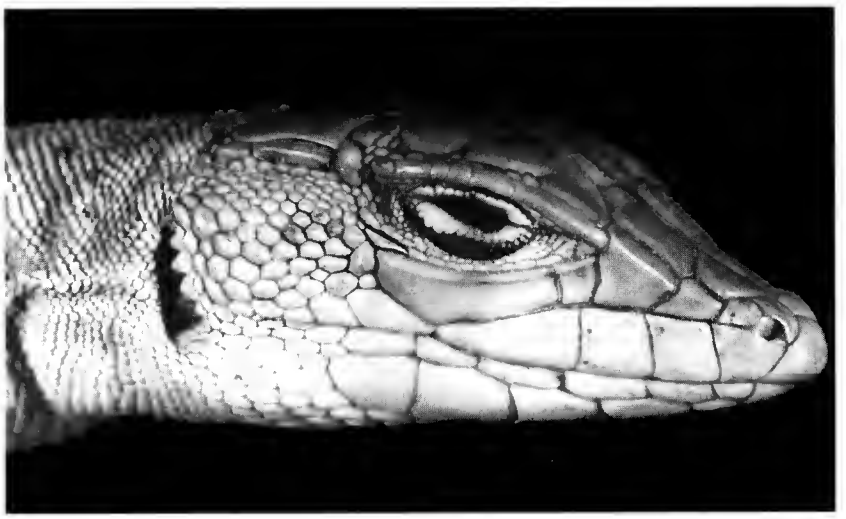

FIG. 2. — Profil, côté droit, de la tête de l'holotype *d'Acanthodactylus taghitensis* n. sp.
Right head profile of the holotype of Acanthodactylus taghitensis *n. sp.*

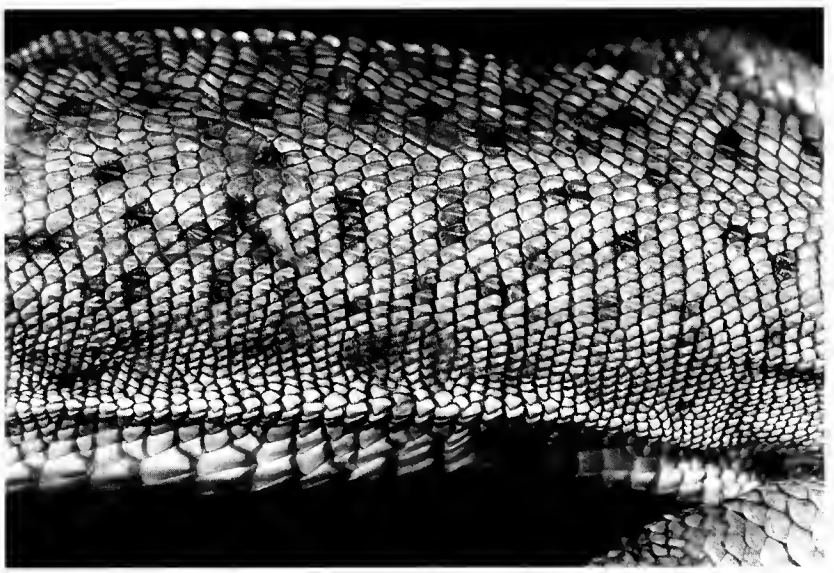

FIG. 3. — Zone dorsolatérale de l'holotype d'*Acanthodactylus taghitensis* n. sp., montrant le passage brusque des grandes écailles du dos aux petites des flancs.
Dorsolateral view of the holotype of Acanthodactylus taghitensis *n. sp. showing sharp demarcation between large scales on back and smaller ones on flanks.*

COMPARAISON AVEC LES AUTRES REPRÉSENTANTS DU GROUPE SCUTELLATUS

L'Acanthodactyle de Taghit présente des caractères communs avec d'autres taxons du groupe *scutellatus* (tabl. I et II) : 4 écailles labiales en avant de la suboculaire (comme chez *Acanthodactylus aureus*) ; taches dorsales sombres reliées longitudinalement par des traits clairs (comme chez *A. aureus*) ; faible nombre (44 et 47) de rangées d'écailles dorsales à mi-corps (comme chez *A. dumerili dumerili* et certains *A. aureus*) ; faible nombre (21) de pores fémoraux (comme chez *A. d. dumerili, A. d. exiguus* et *A. longipes*).

Il se distingue aisément des autres représentants du groupe *scutellatus* par les caractères suivants (cf. tabl. I) : 4 labiales en avant de la suboculaire (fig. 2) (5 chez *A. d. dumerili, A. d. exiguus, A. scutellatus*, 5 ou 6 chez *A. longipes*) ; faible nombre (44 et 47) de rangées d'écailles dorsales à mi-corps (plus de 52 chez *A. s. scutellatus, A. dumerili exiguus* et *A. longipes*, exceptionnellement de 46 à 49 chez *A. scutellatus hardyi*) ; écailles ventrales disposées obliquement en 14 rangées longitudinales à mi-corps (12 perpendiculaires au corps de l'animal chez *A. d. dumerili*, 16 à 18 obliques chez *A. longipes*) ; nombre de pores fémoraux (21) plus élevé que chez *A. d. dumerili* (11 à 20) ; nombre de gulaires comptées longitudinalement (25) plus faible que chez *A. longipes* (de 28 à 43).

Certains caractères morphologiques externes de l'Acanthodactyle de Taghit, lorsqu'ils sont combinés deux à deux, permettent d'originaliser ce lézard sans ambiguïté. De plus, ce taxon

TABLEAU I. — Comparaison de *Acanthodactylus taghitensis* avec les autres Acanthodactyles à 4 rangées d'écailles autour des doigts (d'après ARNOLD, 1983 ; 1986*a* ; 1986*b* ; BONS & GIROT, 1962 ; SALVADOR, 1982 ; LEVITON & ANDERSON, 1967 ; obs. pers.).

TAXONS	1	2	3	4	5	6	7	8	9
Acanthodactylus taghitensis sp. nov.	55	44-47	C	14	O	25	21	19	4
A. aureus Günther, 1903	57	38-60	C	14	O		17-26	21-24	4
A. s. scutellatus (Audouin, 1809)	77	57-87	C	14	O	26-39	16-26	21-28	5
A. s. hardyi Haas, 1957	61	46-62	L	12-14	O				5
A. d. dumerili (Milne Edwards, 1829)	51	38-47	C	12	P		11-20	17-22	5
A. d. exiguus Lataste, 1885	61	53-69	C	14	O		16-25	15-21	5(6)
A. longipes Boulenger, 1918	64	60-97	C	16(18)	O	28-43	22-29	19-26	(5)6
A. cantoris Günther, 1864	77	26-41	C	12-14	P	23-30	19-23	20-24	5
A. blanfordi Boulenger, 1918	75	30-50	C	12-14	P	28-35	14-22	20-23	5
A. schmidti Haas, 1957	105	32-54	C	13-18	P		17-23	21-25	5
A. arabicus Boulenger, 1918	63	27-37	C	14(16)	P	24-32	19-24	20-24	5
A. haasi Leviton & Anderson, 1967	51	36-44	C	12(14)	P	23-25	19-20	26-27	5
A. gongrorhynchatus Lev. & And., 1967	53	56-77	C	10-12	P	34-44	20-25	24-29	4
A. tilburyi Arnold, 1986	60	41-47	C	15-19	P	29-37	20-25	22	5
A. grandis Boulenger, 1909	103	39-64	L/C	14-18	P	22-35	15-24	19-25	4 ou 5
A. masirae Arnold, 1980		34-37	C	10	P	29-33	20-22	23-24	4

1 : Longueur tête-corps maximale (en mm). **2** : Nombre de rangées d'écailles dorsales à mi-corps. **3** : Écailles dorsales carénées (C) ou lisses (L). **4** : Nombre de rangées longitudinales d'écailles ventrales à mi-corps. **5** : Disposition des séries transversales d'écailles ventrales (O = oblique ; P = perpendiculaire au corps de l'animal). **6** : Nombre d'écailles gulaires comptées dans le sens de la longueur. **7** : Nombre de pores fémoraux de chaque côté. **8** : Nombre de lamelles sous le 4^{e} orteil. **9** : Nombre de supralabiales en avant de la suboculaire.

TABLEAU II. — Comparaison d'*Acanthodactylus taghitensis* avec les autres Acanthodactyles à 4 rangées d'écailles autour des doigts (d'après ARNOLD, 1983; 1986*a*; 1986*b*; BONS & GIROT, 1962; SALVADOR, 1982; LEVITON & ANDERSON, 1967; obs. pers.).

Taxons	Remarques	Répartition géographique	Groupe
Acanthodactylus taghitensis sp. nov.	D 2 fois plus grandes que L	Sahara algérien, région de Taghit	*scutellatus*
A. aureus Günther, 1903	D ± de même taille que L	Région littorale atlantique du Sahara	*scutellatus*
A. s. scutellatus (Audouin, 1809)	D ± de même taille que L	Sahara, Palestine	*scutellatus*
A. s. hardyi Haas, 1957	D ± de même taille que L	Arabie saoudite, Koweït, Irak	*scutellatus*
A. d. dumerili (Milne Edwards, 1829)	D ± de même taille que L	Moitié sud de la Mauritanie, Sénégal	*scutellatus*
A. d. exiguus Lataste, 1885	D ± de même taille que L	Tiers occidental du Sahara	*scutellatus*
A. longipes Boulenger, 1918	D ± de même taille que L	Sahara	*scutellatus*
A. cantoris Günther, 1864	D beaucoup plus grandes que L	Afghanistan, N. de l'Inde, N.E. du Pakistan	*cantoris*
A. blanfordi Boulenger, 1918	D plus grandes que L	N. Oman, S. Iran, Pakistan, Afghanistan	*cantoris*
A. schmidti Haas, 1957	D 2 fois plus petites que L	Péninsule d'Arabie, Jordanie, S. W. Iran	*cantoris*
A. arabicus Boulenger, 1918	D 2 fois plus grandes que L	Yémen du Sud, Yémen du Nord	*cantoris*
A. haasi Leviton & Anderson, 1967	D plus grandes que L	Dharan, Sakaka (Arabie saoudite), Oman	*cantoris*
A. gongrorhynchatus Lev. & And., 1967	D un peu plus grandes que L	E. de la péninsule d'Arabie	*cantoris*
A. tilburyi Arnold, 1986	D ± de même taille que L	Riyadh, Al Jawf (Arabie saoudite)	*cantoris*
A. grandis Boulenger, 1909	D ± de même taille que L	N. Arabie, Palestine, Irak, S. W. Iran	*grandis*
A. masirae Arnold, 1980	D ± de même taille que L	Yémen du Sud, Oman	*yemenicus*

D = écailles dorsales; L = écailles latérales.

REMARQUES : Toutes les espèces citées possèdent des écailles temporales carénées à l'exception de *Acanthodactylus grandis* et *A. masirae* chez lesquels elles sont lisses; la suboculaire ne touche pas la lèvre supérieure à l'exception de *A. masirae*; le passage des écailles dorsales aux ventrales s'effectue sans transition ou presque sauf chez *A. gongrorhynchatus*.

possède un critère qui semble unique au sein du groupe *scutellatus* : les écailles dorsales sont environ deux fois plus grandes que les latérales et le passage des dorsales aux latérales s'effectue sans transition (fig. 3). Cette particularité pourrait le rapprocher de certains Acanthodactyles du groupe *cantoris* (*sensu* SALVADOR, 1982; ARNOLD, 1983) qui, cependant, présentent des rangées transversales d'écailles ventrales disposées perpendiculairement au corps de l'animal et non obliquement, possèdent des écailles dorsales plus fortement carénées et s'élargissant progressivement vers l'arrière du dos, et un patron de coloration tout à fait différent.

Acanthodactylus taghitensis n. sp.

HOLOTYPE. — Femelle adulte; 36 km au sud-sud-ouest de Taghit (30°41' N, 2°07' W), région de Beni Abbès, Algérie, 3 novembre 1990. MNHN n° 1995-1201. Récolte : A. FOUCART.

ÉTYMOLOGIE. — *taghitensis*, de Taghit, localité près de laquelle ont été observés les animaux.

DIAGNOSE

Acanthodactyle de taille relativement faible, présentant 4 séries d'écailles autour des doigts, 4 labiales en avant de la suboculaire, des écailles dorsales carénées et relativement peu nombreuses (44 et 47 rangées à mi-corps), deux fois plus grandes sur le dos que sur les flancs et sans zones de transition entre les grandes et les petites; 14 rangées longitudinales d'écailles ventrales disposées en séries transversales obliques; coloration dorsale beige orangé avec 5 rangées longitudinales de points sombres reliés entre eux par des traits clairs longitudinaux.

DESCRIPTION DE L'HOLOTYPE

Dimensions : longueur tête-corps : 55 mm; longueur de la queue (intacte) : 103 mm; longueur de la patte antérieure : 20 mm; longueur patte postérieure : 34 mm; longueur du piléus : 13,1 mm; largeur de la tête : 8,9 mm; hauteur de la tête : 6,8 mm. Pholidose : quatre rangées d'écailles autour des doigts; écaille suboculaire ne bordant pas la lèvre; 4 labiales en avant de la suboculaire, celle-ci en contact avec les supralabiales 4 et 5; 2 granules insérés entre les pariétales; 4 supra-oculaires à droite et à gauche, 1 rangée complète de granules supraciliaires à droite et à gauche, se dédoublant en arrière de la troisième supra-oculaire; 44 rangées d'écailles autour du dos à mi-corps; 30 séries transversales obliques complètes de ventrales disposées en 14 rangées longitudinales à mi-corps; 25 écailles gulaires comptées le long d'une ligne médiane longitudinale; 21 pores fémoraux à droite et à gauche. Les écailles du dos sont tectiformes et carénées; elles sont environ deux fois plus grandes que les écailles des flancs; le passage des écailles dorsales aux latérales s'effectue brusquement.

Coloration : face dorsale beige sable clair; face ventrale blanc pur; le dos est parsemé de petites taches sombres plus ou moins alignées dans le sens de la longueur et reliées dans la moitié antérieure du dos par des traits blanchâtres longitudinaux; les labiales et la suboculaire sont uniformément blanches.

ÉCOLOGIE

Les deux échantillons provenant de deux localités permettent de donner une description sommaire de l'habitat d'*Acanthodactylus taghitensis* : alternance de zones rocheuses et de petites dunes. Le spécimen désigné comme holotype a été capturé dissimulé sous une pierre, au bord d'un petit oued asséché, sur du reg sablonneux avec *Acacia raddiana* et *Launaea arborescens*, à quelque 500 m de la bordure du Grand Erg occidental. Autres reptiles observés dans la deuxième station (5 km au sud-sud-ouest de Taghit) : *Mesalina g. guttulata* (Lichtenstein, 1823), *Uromastyx acanthinurus* Bell, 1825 et *Cerastes* sp. (traces) (M. GENIEZ comm. pers.). Les deux premières espèces citées ne sont pas inféodées au sable.

CONCLUSION

La découverte d'une nouvelle espèce de reptile dans la région de Beni Abbès, pourtant relativement bien connue d'un point de vue herpétologique (*cf.* GAUTHIER 1966, 1967) montre que l'Algérie est un pays incomplètement prospecté. Des recherches dans la région de Taghit permettraient de trouver d'autres spécimens d'*Acanthodactylus taghitensis* et de connaître la morphologie des mâles et des juvéniles.

Remerciements

Les auteurs sont heureux de pouvoir remercier Michel GENIEZ qui a photographié le deuxième spécimen d'*Acanthodactylus taghitensis* et nous a transmis ses observations, M. J. BONS qui nous a fait part de son expérience des Acanthodactyles du groupe *scutellatus*, et J.-Y. QUERO pour les photos de l'holotype.

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Rana (Pelophylax) ridibunda Pallas, 1771, *Rana (Pelophylax) perezi* Seoane, 1885 and their associated klepton (Amphibia, Anura) : morphological diagnoses and description of a new taxon

by Pierre-André CROCHET, Alain DUBOIS, Annemarie OHLER & Heinz TUNNER

Abstract. — Specimens of green frogs from Southern France belonging to the species *Rana (Pelophylax) perezi* Seoane, 1885 and to its associated klepton were identified by enzyme electrophoresis. These specimens, as well as specimens of *Rana (Pelophylax) ridibunda* Pallas, 1771 from Poland, were submitted to a morphometrical analysis, which allowed to find diagnostic measurements and ratios for the three taxa. These allow to confirm the identification of the lectotypes of *Rana fortis* Boulenger, 1884 (currently considered a subjective synonym of *Rana ridibunda*, but which might prove to be a distinct taxon) and of *Rana esculenta perezi*. Both these lectotypes are redescribed. A Latin scientific name and a description are also provided for the klepton associated in Southern France and North-Eastern Spain with *Rana perezi*, and which was until now known as "Graf's frog" or "*Rana* kl. RP".

Keywords. — Green frogs, *Rana ridibunda, Rana perezi*, klepton, Graf's frog, electrophoresis, morphometry, diagnostic measurements and ratios.

Rana (Pelophylax) ridibunda Pallas, 1771, *Rana (Pelophylax) perezi* Seoane, 1885 et leur klepton associé (Amphibia, Anura) : diagnoses morphologiques et description d'un nouveau taxon

Résumé. — Des spécimens de grenouilles vertes du sud de la France appartenant à l'espèce *Rana (Pelophylax) perezi* Seoane, 1885 et à son klepton associé ont été identifiés par électrophorèse de protéines. Ces spécimens, ainsi que des spécimens de *Rana (Pelophylax) ridibunda* Pallas, 1771 de Pologne, ont été soumis à une analyse morphométrique, qui a permis de trouver des mesures et des rapports de mesures diagnostiques pour les trois taxons. Ces critères permettent de confirmer l'identification des lectotypes de *Rana fortis* Boulenger, 1884 (nom actuellement considéré comme un synonyme subjectif de *Rana ridibunda*, mais qui pourrait s'avérer représenter un taxon distinct) et de *Rana esculenta perezi*. Ces deux lectotypes sont redécrits. Un nom scientifique latin et une description sont aussi proposés pour le klepton associé dans le sud de la France et le nord-est de l'Espagne avec *Rana perezi*, et qui était jusqu'à présent connu sous les noms de « grenouille de Graf » ou de « *Rana* kl. RP ».

Mots-clés. — Grenouilles vertes, *Rana ridibunda*, *Rana perezi*, klepton, grenouille de Graf, électrophorèse, morphométrie, mesures et rapports diagnostiques.

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INTRODUCTION

The systematics of European green frogs had a bursting development in the last decades (BERGER, 1973; HOTZ, 1974; DUBOIS, 1977; GÜNTHER, 1979; GRAF & POLLS PELAZ, 1989; GÜNTHER, 1990; DUBOIS & OHLER, 1995*a-b*). The high level of variation occurring among these frogs has been observed for a long time, a fact which is reflected in the very heavy synonymies in this group (DUBOIS & OHLER, 1995*a-b*). Nevertheless, the biological status of the described taxa started being understood only in the beginning of the seventies (TUNNER, 1973). This group contains not only biological species, but also special hybridogenetic taxons, known as kleptons (DUBOIS & GÜNTHER, 1982; DUBOIS, 1991).

A distinct green frog taxon from the Iberian Peninsula and Southern France was described as *Rana esculenta perezi* by SEOANE in 1885. It was long considered to be a subspecies of *Rana ridibunda* (MERTENS & WERMUTH, 1960). An electrophoretic study by GRAF *et al.* (1977) showed not only that it is a distinct species (HOTZ, 1974), but also that it is associated in Southern France with a particular hybridogenetic taxon, which has been named "Graf's frog" (DUBOIS, 1982) or "*Rana* kl. RP" (GRAF & POLLS PELAZ, 1989). The genotype of this klepton is composed of one genome from *Rana perezi* and one genome from *Rana ridibunda* (GRAF & POLLS PELAZ, 1989). The association between *Rana perezi* and Graf's frog was later shown to occur also is the north-eastern part of Spain (UZZELL & TUNNER, 1983; ARANO *et al.*, 1995).

The electrophoretic discrimination between *Rana perezi* and its associated klepton raises no particular problem. However, the morphological determination of these two taxa is not currently possible. For field studies and for studies of fixed collection specimens, it would appear very useful to know morphological characters that would allow to discriminate the two forms. If such characters can be found, they will also allow to check the status of old type-specimens and to solve nomenclatural problems (DUBOIS & OHLER, 1995*a-b*).

In order to explore this question, we carried out a morphometrical study of specimens of green frogs from several localities in Southern France belonging to the species *Rana perezi* and to its associated klepton. These specimens had been ascribed to their respective taxa on the basis of enzyme electrophoresis. The morphometrical analysis allowed to discover several discriminant morphometrical characters for the two taxa. These characters will allow to ascribe old specimens, including types of ancient nominal taxa, to either of the two biological taxa.

For sake of comparison, we took measurements on a series of specimens of *Rana ridibunda* from Poland collected and determined by Leszek BERGER, and we provide information on diagnostic morphometrical characters between this species and the two other green frogs mentioned above.

Rana esculenta perezi was described upon a series of syntypes and the name *perezi* is currently used by specialists of European green frogs for the Iberian and Southern French biological species, *i.e.* the non-hybrid taxon. We had the opportunity to study two of the syntypes of this nominal taxon, including the recently designated lectotype (DUBOIS & OHLER, 1995*a*).

For the associated klepton, we first assumed (DUBOIS & OHLER, 1995*a*) that there was a name available: *Rana maritima* Risso, 1827. This name was based on green frogs from Southern France ("Alpes-Maritimes", as defined at the beginning of the nineteenth century), a region where both *Rana perezi* and Graf's klepton were believed to occur according to the maps published by GRAF & POLLS PELAZ (1989) and CASTANET & GUYÉTANT (1989). Since then, we carried

out field investigations in order to clarify the biological status of frogs in this part of France: these researches showed the occurrence of Italian taxa in this area (DUBOIS & OHLER, 1995*b*; CROCHET *et al.*, in preparation). As a consequence, the name *Rana maritima* Risso, 1827 is available for Italian green frogs, but not for Graf's frog. Resolution of this nomenclatural problem leaves no more name available for Graf's frog, so that we are led to name it in this paper.

A description of the lectotype of *Rana fortis* Boulenger, 1884 (DUBOIS & OHLER, 1995*a*) is also included in this paper. The taxon *Rana ridibunda* as currently understood is probably heterogeneous (GÜNTHER, 1982). Mating calls of *Rana ridibunda* from the Caspian Sea region (type-locality) were recorded and studied (SCHNEIDER & EGIASARJAN, 1991) and compared with those from various East European and West Asian regions (SCHNEIDER & SINSCH, 1992), and no significant differences were found. However, no such comparisons were made involving mating calls recorded in Central, Northern and Western Europe. Obvious differences in general aspect, colours and size, between frogs from the latter areas and those from East Europe and Asia point to the possible existence of two distinct species. Future works, using various methods (morphology, protein electrophoresis, caryology, bioacoustics, etc.) will have to address this question. If a distinct species had to be recognized for the European frogs, it should bear the scientific name *Rana (Pelophylax) fortis* (see DUBOIS & OHLER, 1995*a*). The specimens from Poland that we examined in this study are typical for the Central and Western European populations currently referred to *Rana ridibunda*, that include also the Berlin frogs for which the name *Rana fortis* had been proposed.

MATERIAL AND METHODS

ABBREVIATIONS. — MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN : Muséum national d'Histoire naturelle, Paris, France; SVL : Snout-vent length.

SPECIMENS STUDIED. — The specimens listed below were measured. Specimens were also studied by electrophoresis, except those whose number is followed below by an asterisk (*). Juveniles, followed below by the sign #, were used only for the computation of values shown in Fig. 2, but not of values given in Table II.

Rana perezi Seoane, 1885. — **France**: (A) Pyrénées-Orientales: Banyuls-sur-Mer (42°28'N, 3°07'E): MNHN 1993.3377-3381 (2 adult males and 3 adult females), coll. Jean-Daniel GRAF, March 1976; (B) Bouches-du-Rhône: (1) Faraman (43°25'N, 4°43'E), 2.5 km west of Salin-de-Giraud: MNHN 1991.77, 1991.83, 1991.88 and 1991.94 (adult males), 1991.84#, 1991.87#, 1991.89-93# and 1991.95-96# (5 juvenile males and 4 juvenile females), coll. Alain DUBOIS, 8 September 1977; (2) Fumemorte (43°28'N, 4°42'E), 6 km north of Salin-de-Giraud: MNHN 1991.677 (adult male), 1991.676# and 1991.678# (juvenile male and juvenile female), coll. Alain DUBOIS, 8 September 1977; (3) Saint-Bertrand (43°27'N, 4°39'E), 7 km north-west of Salin-de-Giraud: MNHN 1991.675 (adult female), coll. Alain DUBOIS, 8 September 1977; (4) Collocation (43°26'N, 4°41'E), 3.5 km north-west of Salin-de-Giraud: MNHN 1991.680 (adult male), 1991.679# (juvenile male), coll. Alain DUBOIS, 8 September 1977; (5) Astouin (43°32'N, 4°24'E), 10 km north of Saintes-Maries-de-la-Mer: MNHN 1991.97# (juvenile female), coll. Alain DUBOIS, 5 September 1977; (6) Bac du Petit Sauvage (43°29'N, 4°25'E), 5 km north-west of Saintes-

Maries-de-la-Mer: MNHN 1991.100#, 1991.670# and 1991.672-673# (3 juvenile males and 1 juvenile female), coll. Alain DUBOIS, 5 September 1977. — **Spain**: Galicia: La Coruña: (1) La Coruña (43°22'N, 8°23'W): MCZ 6832* (adult female), coll. D. Victor LOPEZ SEOANE, lectotype of *Rana esculenta perezi*; (2) Cabañas (43°24'N, 8°09'W): MNHN 1889.596* (adult female), coll. D. Victor LOPEZ SEOANE, paralectotype of *Rana esculenta perezi*.

Rana "kl. RP" (GRAF & POLLS PELAZ, 1989). — **France**: (A) Gard: Gorges de l'Aiguillon, between Lussan (44°09'N, 4°22'E) and La Bastide: MNHN 1993.3374-3376 (adult females), coll. Jean-Daniel GRAF, March 1976; (B) Bouches-du-Rhône: (1) Faraman (43°25'N, 4°43'E), 2.5 km west of Salin-de-Giraud: MNHN 1991.76 and 1991.78 (adult females), 1991.79-80 and 1991.82 (subadult females), 1991.85 (juvenile male) and 1991.86 (adult male), coll. Alain DUBOIS, 8 September 1977; (2) Astouin (43°32'N, 4°24'E), 10 km north of Saintes-Maries-de-la-Mer: MNHN 1991.98-99# (juvenile males), coll. Alain DUBOIS, 5 September 1977; (3) Bac du Petit Sauvage (43°29'N, 4°25'E), 5 km north-west of Saintes-Maries-de-la-Mer: 1991.671# and 1991.674# (juvenile males), coll. Alain DUBOIS, 5 September 1977.

Rana ridibunda Pallas, 1771. — **Germany**: Berlin (52°32'N, 13°24'E), lake-like expansion of the river Spree: MNHN 1884.254* (adult female), 1884.255* and 1884.256* (adult males), coll. fisherman NOACK, spring 1884, respectively paralectotype, lectotype and paralectotype of *Rana fortis* Boulenger, 1884. — **Poland**: Poznan Debina: MNHN 1982.2340* (adult female), 1982.2349* (adult male), 1982.2372-2373* (subadult females), 1982.2379* (subadult male), coll. Leszek BERGER, 20 August 1968.

ELECTROPHORESIS. — The specimens of *Rana perezi* and of its associated klepton were identified by electrophoresis, except for old type-specimens. Those from Gard (Gorges de l'Aiguillon) and from Pyrénées-Orientales (Banyuls-sur-Mer) were part of those studied and reported upon by GRAF *et al.* (1977), for which the following enzyme loci were studied: LDH-B, CK, AAT-1 and AAT-2. Those from Bouches-du-Rhône (Camargue) were identified on the basis of LDH alone, which is clearly diagnostic for the distinction of the two taxa; the method used for this electrophoresis is described in TUNNER (1980: 261-262).

MEASUREMENTS. — Twenty-six measurements (Table I) were taken from all specimens with caliper or binocular microscope. Except for *Rana ridibunda*, only electrophoretically determined adults and subadults were included in the morphometrical analysis which led to values given in Table II. Since the aim of this work was to find diagnostic measurements, we discarded in the results those measurements and ratios which did not show significant differences between the three frog taxa studied.

STATISTICS. — Despite the low numbers of specimens studied, these numbers are enough for a statistical analysis using non-parametric tests with a level of significance of .001 (see *e.g.* DUBOIS, 1984). Mean, standard deviation and range were computed for all variables of all groups on a personal computer with SPSS program (NORUSIS, 1992). The standard non-parametric Mann-Whitney U test (ZAR, 1984) was used to compare the three groups pairwise.

To compare ratios from adult-subadult and juvenile specimens, we used boxplot sketches (NORUSIS, 1992). These boxplots display summary statistics for the distribution and plot the median, the 25th percentile, the 75th percentile and values more than 1.5 box-lengths from 75th percentile (outliers).

TABLE I. – Description of measurements.
Description des mensurations.

EL	Eye length
EN	Distance from eye to nostril
FLL	Forelimb length (from elbow to base of outer palmar tubercle)
FOTL	Fourth toe length (from base of outer metatarsal tubercle)
HL	Head length (from mandibular articulation to tip of snout)
HW	Head width
IBE	Distance between posterior edges of eyes
IC	Distance between choanae
IFE	Distance between anterior edges of eyes
IMT	Length of inner metatarsal tubercle
IMTH	Height of inner metatarsal tubercle
IN	Internarial space
ITL	Inner toe length (from distal edge of inner metatarsal tubercle)
IV	Distance between proximal edges of vomerine ridges
MBE	Distance from mandibular articulation to posterior edge of eye
MFE	Distance from mandibular articulation to anterior edge of eye
MN	Distance from mandibular articulation to nostril
SVL	Snout-vent length
TFL	Third finger length (from base of proximal subarticular tubercle)
TL	Tibia length
TYD	Greatest tympanum diameter
TYE	Distance from tympanum to back of eye
VRL	Length of vomerine ridge
VTL	Distance between distal edges of vomerine ridges
WOFF	Webbing between fourth and fifth toe (from base of outer metatarsal tubercle)
WOTF	Webbing between third and fourth toe (from base of outer metatarsal tubercle)

NOMENCLATURE OF KLEPTONS. — For the nomenclatural treatment of kleptons, we follow the proposals of DUBOIS & GÜNTHER (1982) and DUBOIS (1991), according to which kleptons are taxa of the species-group that are nomenclaturally of the species rank but that have biological properties different of those of "biological species" ("normal", bisexual species). Kleptons receive scientific Latin names similar to those of species, but which can be distinguished from the latter by the insertion of the sign "kl." between the genus-group name(s) and the species-group name(s). We follow DUBOIS & OHLER (1995*a*) in their placement of European green frogs in the subgenus *Pelophylax* Fitzinger, 1843 of the genus *Rana* Linnaeus, 1758.

DESCRIPTIVE METHODS. — In order to facilitate comparisons, the detailed descriptions of the three type-specimens given below follow the same plan. Webbing formula is presented according to MYERS & DUELLMAN (1982).

RESULTS

MORPHOMETRICAL COMPARISONS OF *RANA PEREZI, RANA RIDIBUNDA* AND GRAF'S FROG

Electrophoretic data obtained from the specimens collected in Bouches-du-Rhône, Gard and Pyrénées-Orientales allowed to refer clearly these specimens to two taxa: *Rana perezi* and its associated hybridogenetic klepton (see GRAF *et al.*, 1977; GRAF & POLLS PELAZ, 1989). For

the research of diagnostic measurements, we pooled all specimens electrophoretically characterized, irrespective of their sexes, ages and localities: thus we had 12 adult and subadult specimens of *Rana perezi* and 9 adult and subadult specimens of Graf's klepton.

Thirty-seven ratios were tested pairwise with the Mann-Whitney U test. Fourteen ratios were found to be diagnostic between *Rana perezi* and Graf's frog (Table II). These measurements are from various parts of the body: head, foot and webbing. Particularly interesting and diagnostic are the measurements which involve the vomerine ridges. The ratios IV/VRL, IV/IC, IV/SVL and also WOTF/FOTL show highly significant differences between our two samples. *Rana perezi* has a greater distance between vomerine ridges (Fig. 1), which appears in the ratios involving IV. It also has a longer foot and a less developed webbing.

The sample of the hybridogenetic klepton is statistically different from *Rana ridibunda* for 16 ratios (Table II). The measurements involve also the different parts of the body. The ratios TYD/IN, TYD/SVL, TYE/SVL and VRL/IC show rather high significant differences between the two samples. *Rana ridibunda*'s tympanum is relatively smaller than in both *Rana perezi* and Graf's frog. The distance between vomerine ridges is somewhat intermediate. *Rana ridibunda* shows the highest development of webbing of the three forms.

Twelve ratios describing the two groups representing *Rana ridibunda* and *Rana perezi* show statistically significant differences (Table II). Seven of these ratios (HW/SVL, IV/IC, IV/VRL, TYD/SVL, TYD/TYE, WOTF/FOTL, WOTF/SVL) show rather high significant differences between the two samples. *Rana perezi* has a clearly narrower head than *Rana ridibunda*, a larger tympanum and tympanum-eye distance, and less webbing on feet. Vomerine ridges and associated features are more separated than in *Rana ridibunda*.

Five ratios show significant differences between all three groups (IV/IC, IV/SVL, IV/VRL, TYD/SVL, TYD/TYE). They concern vomerine ridges' position and tympanum size. Foot measurements of *Rana* kl. RP show intermediate values between *Rana ridibunda* and *Rana perezi*. But the values for vomerine teeth morphology are intermediate in *Rana ridibunda* and extreme in the hybrid.

Some ratios, which are clearly diagnostic between *Rana perezi* and Graf's frog in adults, can also be used cautiously for determination of juveniles of these two forms, as shown here in Fig. 2 for the ratio IV/VRL: out of 42 specimens studied, only one showed an ambiguous value for this ratio.

Of the ratios diagnostic for the complex *Rana lessonae* – *Rana* kl. *esculenta* – *Rana ridibunda* (BERGER, 1973), only one, TL/SVL, shows a significant statistical difference between *Rana ridibunda* and *Rana perezi*.

STUDY OF TWO SYNTYPES OF *RANA ESCULENTA PEREZI* SEOANE, 1885

We were able to study and measure two of the original syntypes of *Rana esculenta perezi* and we computed the ratios shown above to allow morphological distinction of the three taxa studied. Table III shows that the values of most of these ratios fall within the ranges of *perezi*. We conclude that these two syntypes are morphologically similar to the electrophoretically characterized specimens of *Rana perezi*. Designation by DUBOIS & OHLER (1995*a*) of one of these two syntypes as lectotype of *perezi* was therefore appropriate to stabilize definitely the nomenclatural status of this name. A detailed description of this lectotype is provided below.

DESCRIPTIONS OF TYPE-SPECIMENS

Rana (Pelophylax) kl. **grafi** kl. nov.
(Figs 1a, 3)

HOLOTYPE. — MNHN 1993.3374, adult female (SVL 111.0 mm), collected by Jean-Daniel GRAF in the Gorges de l'Aiguillon, between Lussan (44°09'N, 4°22'E) and La Bastide, Gard, France, in March 1976.

PARATYPES. — MNHN 1993.3375-3376, adult females (SVL 94.5 mm and 56.9 mm), same collection data as the holotype. MNHN 1991.76, adult female (SVL 71.9 mm), 1991.78, adult female (SVL 66.5 mm), 1991.79-80, subadult females (SVL 91.0 and 71.2 mm), 1991.82, subadult female (SVL 55.2 mm), 1991.85, juvenile male (SVL 39.2 mm) and 1991.86, adult male (SVL 33.9 mm), collected by Alain DUBOIS at Faraman (43°25'N, 4°43'E), 2.5 km west of Salin-de-Giraud, Bouches-du-Rhône, France, on 8 September 1977. MNHN 1991.98-99, juvenile males (SVL 27.6 mm and 36.5 mm), collected by Alain DUBOIS at Astouin (43°32'N, 4°24'E), 10 km north of Saintes-Maries-de-la-Mer, Bouches-du-Rhône, France, on 5 September 1977. MNHN 1991.671 and 1991.674, juvenile males (SVL 29.9 mm and 24.9 mm), collected by Alain DUBOIS near the Bac du Petit Sauvage (43°29'N, 4°25'E), 5 km north-west of Saintes-Maries-de-la-Mer, Bouches-du-Rhône, France, on 5 September 1977.

NOTE ON PARATYPES. — Paratypes are morphologically similar to the holotype.

ETYMOLOGY OF SPECIES-GROUP NAME. — We dedicate this frog to Jean-Daniel GRAF who discovered this new klepton and kindly provided us with some of the specimens he had studied by electrophoresis.

DIAGNOSIS

A large-sized green frog. It can be distinguished morphologically from *Rana perezi* by more webbing on feet and higher metatarsal tubercle. It differs from *Rana ridibunda* by its smaller head width, eye-tympanum distance smaller than half of tympanum diameter, shorter fourth toe and lesser webbing. Of both taxa, Graf's frog is distinguished by its smaller intervomer distance, longer vomerine teeth ridges and smaller ratio of vomerine ridge length by intervomer distance. Electrophoretic characteristics of this taxon were published by GRAF *et al.* (1977).

DESCRIPTION OF HOLOTYPE

Specimen with tissue sampling, snout-vent length 111.0 mm. Head slightly longer (35.2 mm) than broad (34.0 mm); snout moderately pointed, slightly protruding beyond mouth, slightly shorter (8.2 mm) than diameter of eye (8.6 mm); canthus rostralis rounded, loreal region abrupt, concave; interorbital space flat, smaller (4.3 mm) than both internarial distance (5.1 mm) and upper eyelid width (6.8 mm); nostril slightly nearer (7.4 mm) to eye than to tip of snout (8.2 mm); tympanum present, its diameter (6.9 mm) more than two third of diameter of eye, its distance to eye (5.1 mm) roughly three fourth of its diameter; vestige of pineal eye absent; tongue ovally elongated, emarginated behind, finely granulated. Vomerine teeth between choanae in two ridges forming an angle of 150°; ridges long (6.3 mm), 63.0 times the separation between them (0.1 mm).

Arm short, forearm (19.8 mm) shorter than hand (23.5 mm); finger length, shortest to longest: II < I < IV < III; length of third finger 13.8 mm; tips of fingers pointed; three metacarpal tubercles, moderately developed; supernumerary tubercle on base of finger III; subarticular tubercles rounded, moderately developed.

Hind limbs moderately long, shank three times longer (48.2 mm) than broad (15.1 mm), slightly shorter than thigh (50.9 mm); shank and thigh both shorter than distance from base of inner metatarsal tubercle to tip of toe IV (51.6 mm); toes moderately long, length of IV (30.6 mm)

TABLE II. — Results of Mann-Whitney U-test comparing some morphometric ratios of adults and subadults of *Rana perezi* (P; n = 13), *Rana* kl. *grafi* (G; n = 8) and *Rana ridibunda* (R; n = 5). Ranges, mean and standard deviation are given for each species. Significance level : *** 0.001; ** 0.010; * 0.050.

Résultats de la comparaison par le test U de Mann-Whitney de quelques rapports morphométriques chez des adultes et subadultes de Rana perezi *(P ; n = 13),* Rana *kl.* grafi *(G ; n = 8) et* Rana ridibunda *(R ; n = 5). Pour chaque espèce sont données les valeurs extrêmes du rapport, la moyenne et l'écart-type. Coefficients de risque : *** 0.001 ; ** 0.010 ; * 0.050.*

Ratio	*Rana perezi*	*Rana* kl. *grafi*	*Rana ridibunda*	P × R	P × G	R × G
FOTL/SVL	0.560 ± 0.053 0.479 – 0.632	0.536 ± 0.042 0.455 – 0.588	0.582 ± 0.015 0.556 – 0.595			*
HW/SVL	0.341 ± 0.012 0.322 – 0.359	0.351 ± 0.024 0.306 – 0.393	0.376 ± 0.015 0.353 – 0.393	**		*
IBE/SVL	0.236 ± 0.021 0.192 – 0.268	0.314 ± 0.017 0.179 – 0.230	0.221 ± 0.017 0.204 – 0.239		*	
IC/SVL	0.099 ± 0.010 0.082 – 0.115	0.086 ± 0.007 0.071 – 0.097	0.096 ± 0.005 0.091 – 0.102		*	*
IMT/SVL	0.051 ± 0.006 0.038 – 0.059	0.054 ± 0.006 0.048 – 0.065	0.047 ± 0.006 0.044 – 0.057			*
IN/SVL	0.069 ± 0.009 0.053 – 0.084	0.058 ± 0.007 0.046 – 0.069	0.062 ± 0.006 0.056 – 0.069		**	
IV/IC	0.11 ± 0.03 0.066 – 0.171	0.03 ± 0.02 0.013 – 0.060	0.06 ± 0.01 0.046 – 0.073	**	***	*
IV/SVL	0.011 ± 0.004 0.006 – 0.018	0.003 ± 0.002 0.001 – 0.005	0.006 ± 0.001 0.004 – 0.007	*	***	*
IV/VRL	0.346 ± 0.139 0.192 – 0.692	0.008 ± 0.004 0.003 – 0.016	0.158 ± 0.032 0.123 – 0.200	**	***	*
THL/SVL	0.494 ± 0.029 0.448 – 0.559	0.517 ± 0.022 0.467 – 0.534	0.781 ± 0.023 0.457 – 0.509		*	*
TL/SVL	0.507 ± 0.034 0.445 – 0.557	0.531 ± 0.037 0.459 – 0.574	0.551 ± 0.018 0.525 – 0.566	*		
TYD/IN	1.34 ± 0.30 1.00 – 2.00	1.86 ± 0.19 1.61 – 2.22	1.11 ± 0.10 0.973 – 1.19		**	**
TYD/SVL	0.091 ± 0.008 0.081 – 0.108	0.106 ± 0.005 0.099 – 0.111	0.069 ± 0.003 0.066 – 0.072	**	**	**
TYD/TYE	2.86 ± 0.71 1.79 – 4.25	2.16 ± 0.21 1.83 – 2.39	1.88 ± 0.22 1.68 – 2.25	**	*	*
TYE/SVL	0.034 ± 0.011 0.021 – 0.049	0.050 ± 0.006 0.044 – 0.059	0.037 ± 0.005 0.029 – 0.042		*	**
VRL/IC	0.34 ± 0.07 0.246 – 0.480	0.43 ± 0.04 0.365 – 0.482	0.36 ± 0.02 0.336 – 0.373		**	**
VRL/SVL	0.047 ± 0.018 0.026 – 0.073	0.080 ± 0.023 0.057 – 0.132	0.069 ± 0.007 0.059 – 0.074	*	**	
WOFF/SVL	0.339 ± 0.034 0.291 – 0.400	0.364 ± 0.034 0.312 – 0.405	0.384 ± 0.012 0.368 – 0.402	*		*
WOTF/FOTL	0.59 ± 0.06 0.435 – 0.648	0.67 ± 0.03 0.617 – 0.715	0.68 ± 0.02 0.638 – 0.697	**	***	
WOTF/SVL	0.330 ± 0.035 0.284 – 0.397	0.358 ± 0.026 0.312 – 0.386	0.394 ± 0.010 0.380 – 0.405	**		*
WOTF/WOFF	0.976 ± 0.046 0.899 – 1.05	0.987 ± 0.033 0.945 – 1.06	1.03 ± 0.020 1.01 – 1.06	*		*

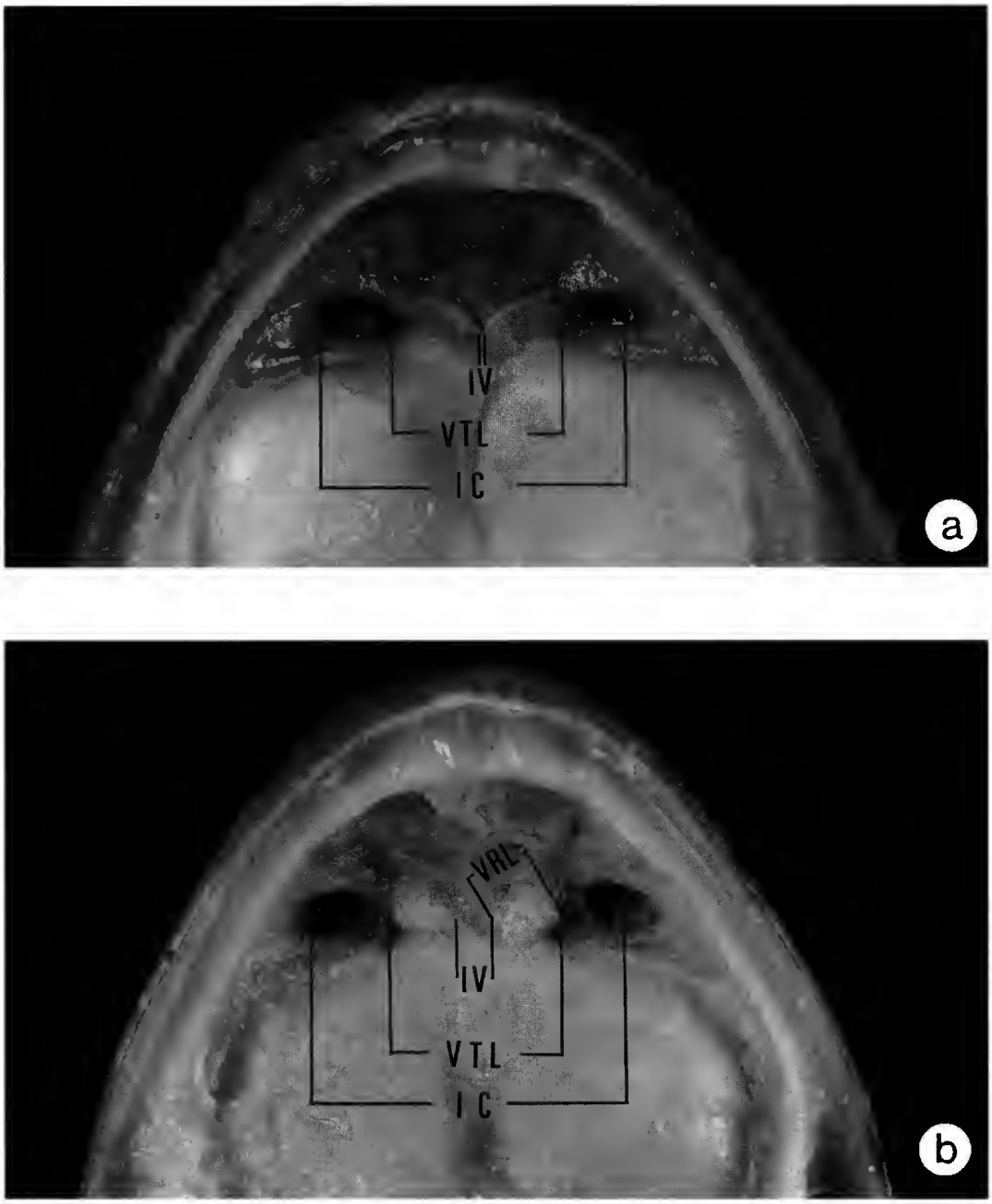

FIG. 1. — Vomerine teeth position in (a) *Rana* kl. *grafi* (MNHN 1993.3374, holotype) and (b) *Rana perezi* (MNHN 1993.3377). Scale: 5 mm. For the meaning of abbreviations, see Table I.

Position des dents vomériennes chez (a) Rana *kl.* grafi *(MNHN 1993.3374, holotype) et (b)* Rana perezi *(MNHN 1993.3377). Échelle : 5 mm. Pour la signification des abréviations, voir le tableau I.*

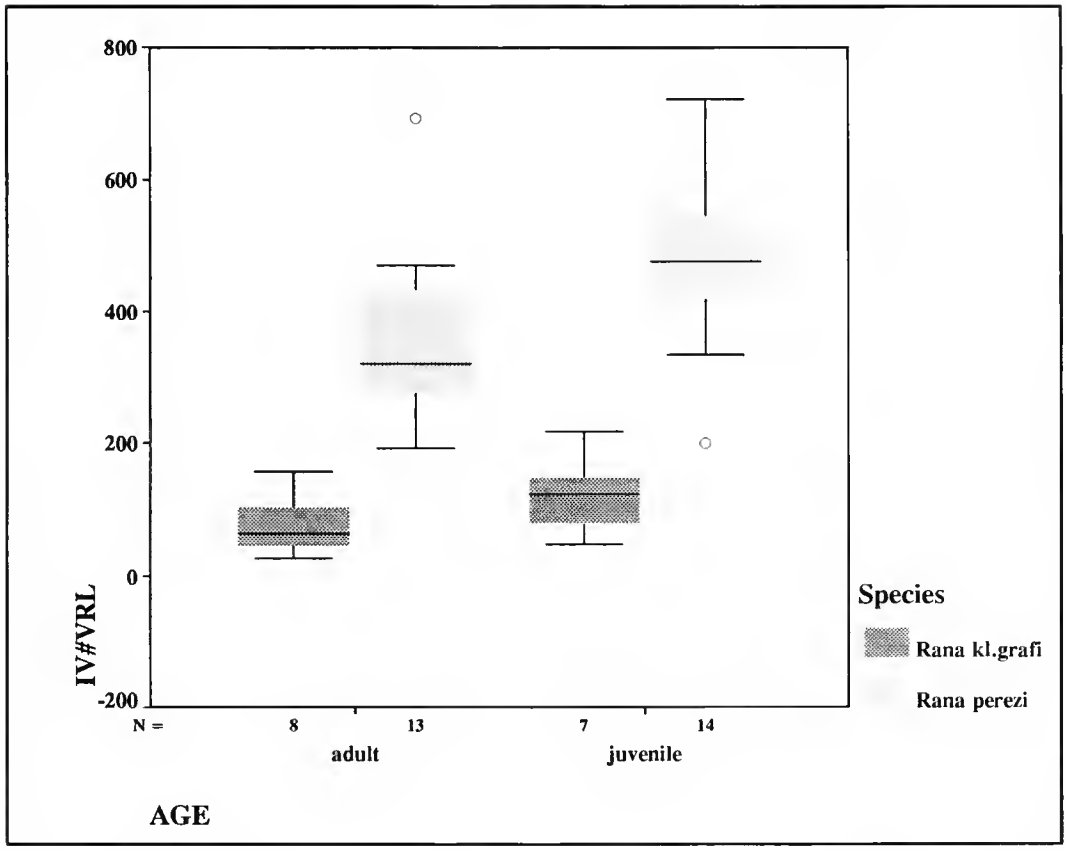

FIG. 2. — Boxplot sketches displaying summary statistics for the ratio IV/VRL in adult-subadult and juvenile specimens of *Rana* kl. *grafi* and *Rana perezi*. The median, the 25th percentile, the 75th percentile and outliers are plotted. N: number. For the meaning of other abbreviations, see Table I.

Diagramme « boxplot » montrant les paramètres statistiques principaux pour le rapport IV/VRL chez des spécimens adultes-subadultes et juvéniles de Rana *kl.* grafi *et* Rana perezi. *La médiane, le 25e percentile, le 75e percentile et les valeurs excentriques (« outliers ») sont figurés. N: nombre. Pour la signification des autres abréviations, voir le tableau I.*

less than one half of length from base of tarsus to tip of toe IV (72.6 mm); tips of toes rounded; webbing moderately developed (I 1/2 – 1 II 1/2 – 1 1/2 III 1/2 – 1 1/2 IV 1 – 1/2 V); inner metatarsal tubercle moderately developed, its length (5.3 mm) 2.9 times in length of toe I (15.5 mm); glandular ridge on tarsus prominent.

Dorsum with large flat warts, also between eyes; two broad glandular dorsolateral ridges; ventral surfaces smooth.

Colour in alcohol: Brownish with few large darker spots; a slightly clearer mediodorsal line; dorsolateral folds darker brown; forelimbs without darker spots; hind limbs with few darker bands; ventral surface cream and brown marbled, blurred; back of thigh dark brown with brown spots.

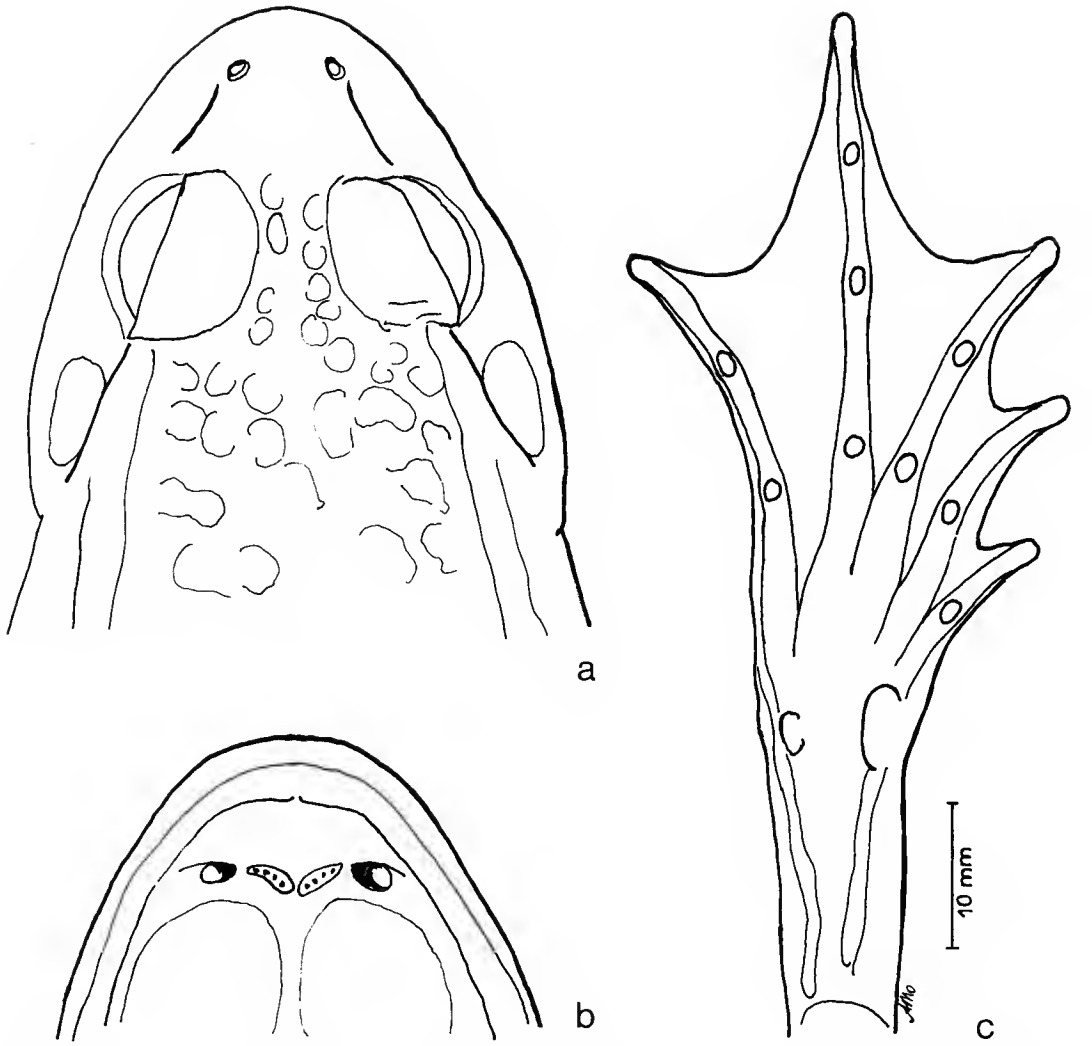

FIG. 3. — *Rana (Pelophylax)* kl. *grafi* kl. nov., MNHN 1993.3374 (holotype): (a) dorsal view of head; (b) roof of mouth; (c) ventral view of right foot.

Rana (Pelophylax) *kl.* grafi *kl. nov., MNHN 1993.3374 (holotype): (a) vue dorsale de la tête; (b) plafond buccal; (c) vue ventrale du pied droit.*

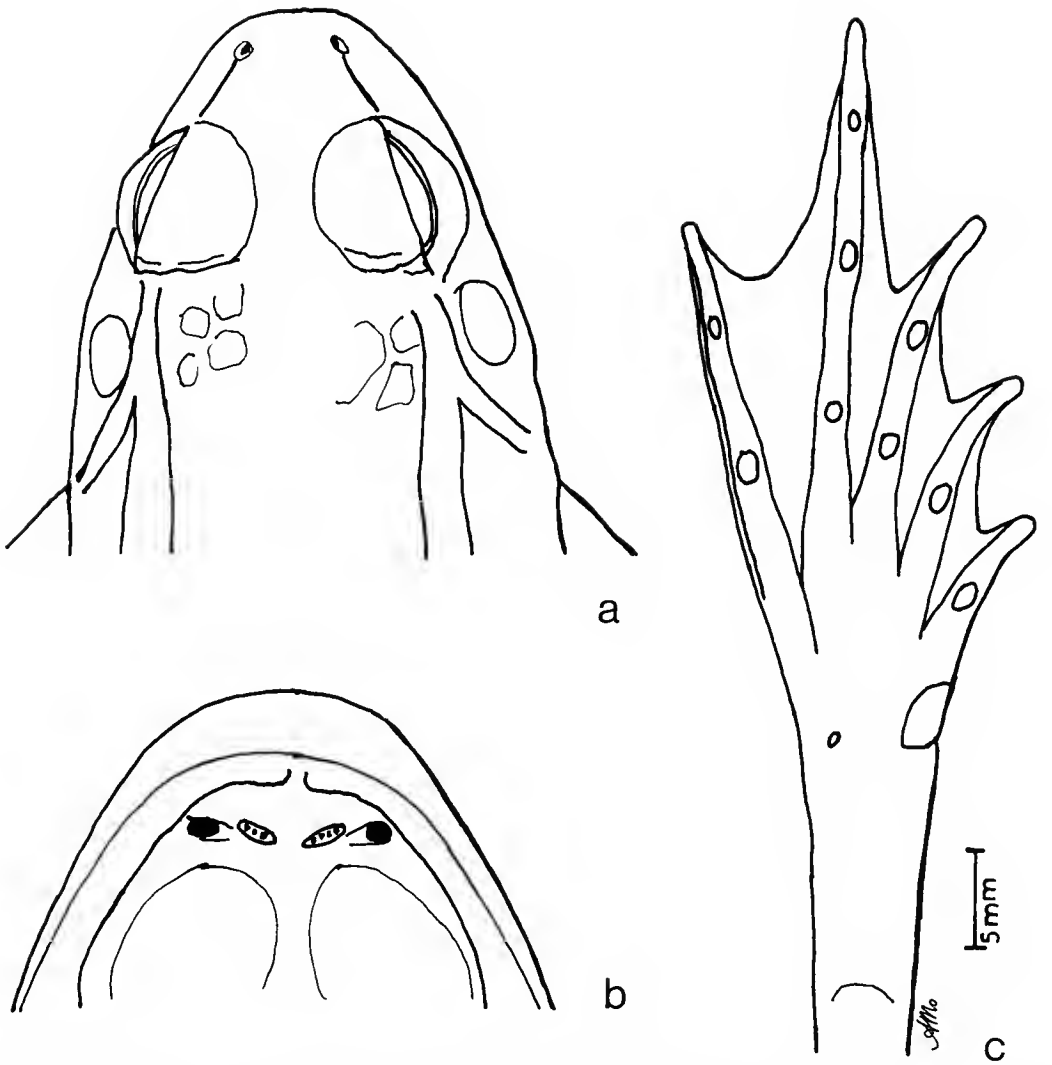

FIG. 4. — *Rana (Pelophylax) perezi* Seoane, 1885, MCZ 6832 (lectotype): (a) dorsal view of head; (b) roof of mouth; (c) ventral view of right foot.

Rana (Pelophylax) perezi *Seoane, 1885, MCZ 6832 (lectotype): (a) vue dorsale de la tête; (b) plafond buccal; (c) vue ventrale du pied droit.*

Rana (Pelophylax) perezi Seoane, 1885
(Figs 1b, 4)

LECTOTYPE (BY DESIGNATION OF DUBOIS & OHLER, 1995a) OF *RANA ESCULENTA PEREZI* SEOANE, 1885: 171. — MCZ 6832, adult female (SVL 63.6 mm), collected by D. Victor LOPEZ SEOANE near La Coruña (43°22'N, 8°23'W), Galicia, Spain, from Fernand LATASTE's collection.

PARALECTOTYPE OF *RANA ESCULENTA PEREZI* SEOANE, 1885: 171. — MNHN 1889.596, adult female (SVL 71.5 mm), from Cabañas (43°24'N, 8°09'W), Galicia, Spain, donation of Victor LOPEZ SEOANE to the Paris Museum on 9 November 1889.

NOTE ON PARALECTOTYPE. — The paralectotype studied is similar to the lectotype, except that it shows an asymmetry in its vomerine teeth. Other paralectotypes may possibly be found in the future, in other Museums where SEOANE or LATASTE may have deposited some of the original syntypes of this taxon.

DIAGNOSIS

A medium-sized green frog. It can be distinguished morphologically from *Rana* kl. *grafi* by less webbing on its feet and its smoother metatarsal tubercle. It differs from *Rana ridibunda* by its smaller head, tympanum closer to eye, shorter hand and foot. It has a larger intervomer distance than both *Rana ridibunda* and *Rana* kl. *grafi*.

DESCRIPTION OF LECTOTYPE

Well-preserved specimen, snout-vent length 63.6 mm. Head slightly longer (22.9 mm) than broad (21.8 mm); snout rounded, not protruding beyond mouth, longer (10.4 mm) than diameter of eye (7.7 mm); canthus rostralis rounded, loreal region abrupt, concave; interorbital space flat, smaller (1.9 mm) than both internarial distance (4.2 mm) and upper eyelid width (4.6 mm); nostril slightly nearer (4.8 mm) to eye than to tip of snout (5.3 mm); tympanum present, its diameter (4.1 mm) more than half of diameter of eye, its distance to eye (1.4 mm) roughly one third of its diameter; vestige of pineal eye absent, tongue ovally elongated, deeply emarginated behind, finely granulated. Vomerine teeth between choanae in two ridges forming an angle of 140°; ridges long (1.94 mm), 3.1 times the separation between them (0.62 mm).

Arm short, forearm (11.2 mm) shorter than hand (14.2 mm); finger length, shortest to longest: I < II < IV < III; length of third finger 8.5 mm; tips of fingers pointed; metacarpal tubercles not distinct, subarticular tubercles rounded, moderately developed.

Hind limbs relatively short, shank almost three times longer (28.3 mm) than broad (11.3 mm), slightly shorter than thigh (29.1 mm); shank and thigh both shorter than distance from base of inner metatarsal tubercle to tip of toe IV (34.6 mm); toes moderately long, length of IV (19.2 mm) less than one third of length from base of tarsus to tip of toe IV (46.9 mm); tips of toes pointed; webbing moderately developed (I 1/2 – 2 II 1 – 2 III 1 – 2 IV 2 – 1 V); inner metatarsal tubercle moderately developed, its length (3.6 mm) 2.3 times in length of toe I (8.3 mm); glandular ridge on tarsus flat.

Dorsum with large flat warts, except on top of head; two broad glandular dorsolateral ridges; ventral surfaces smooth.

Colour in alcohol: Brownish with few large darker spots; a slightly clearer mediodorsal line; dorsolateral folds slightly darker brown; forelimbs with few darker spots; hind limbs with darker spotlike bands; ventral surface cream and brown marbled, very homogeneous; back of thigh blackish with few clearer spots, a dark line separating ventral from dorsal surface.

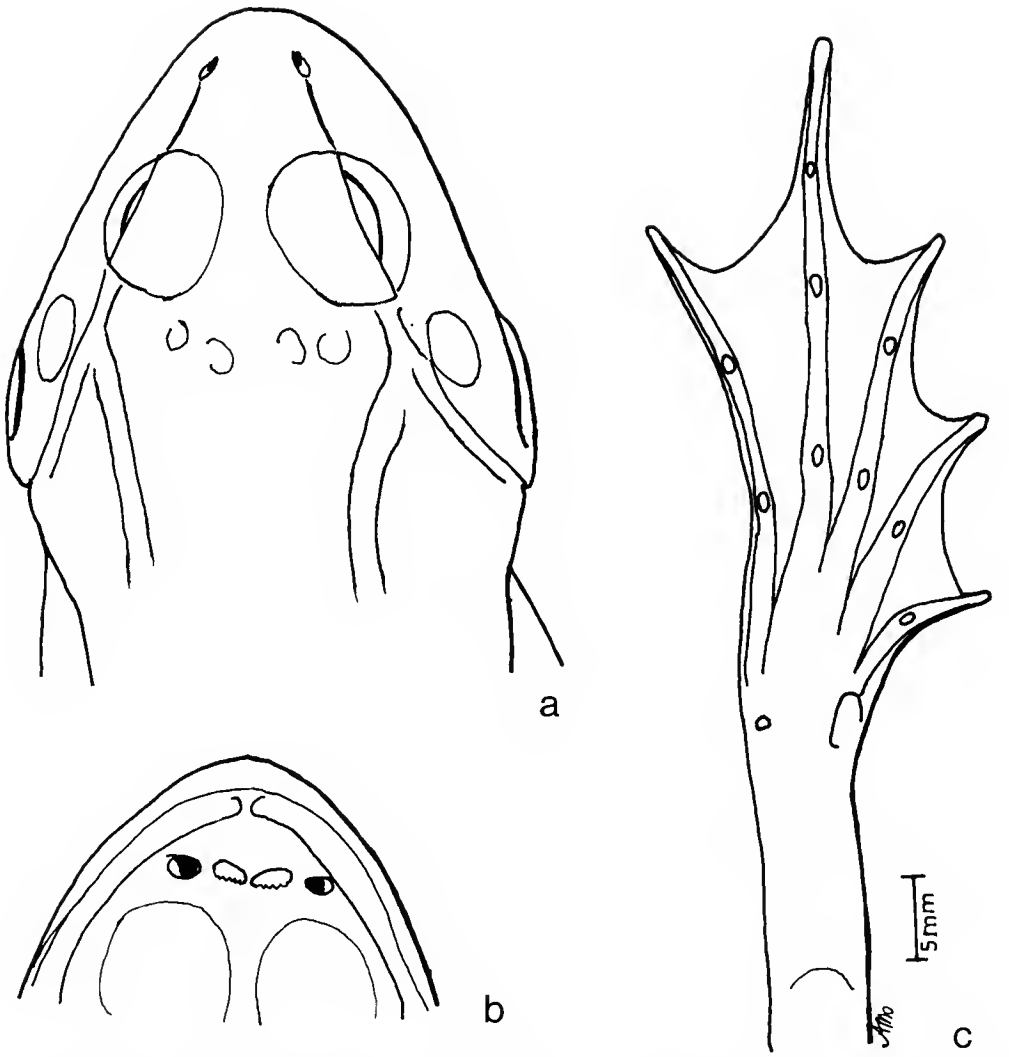

FIG. 5. — *Rana (Pelophylax) ridibunda* Pallas, 1771, MNHN 1884.255 (lectotype of *Rana fortis* Boulenger, 1884): (a) dorsal view of head; (b) roof of mouth; (c) ventral view of right foot.

Rana (Pelophylax) ridibunda *Pallas, 1771, MNHN 1884.255 (lectocype de* Rana fortis *Boulenger, 1884): (a) vue dorsale de la tête; (b) plafond buccal; (c) vue ventrale du pied droit.*

Rana (Pelophylax) ridibunda Pallas, 1771
(Fig. 5)

LECTOTYPE (BY DESIGNATION OF DUBOIS & OHLER, 1995*a*) OF *RANA FORTIS* BOULENGER, 1884: 220. — MNHN 1884.255, adult male (SVL 71.4 mm), collected by fisherman NOACK in a lake-like expansion of the river Spree, near Berlin, Berlin, Germany.

PARALECTOTYPES OF *RANA FORTIS* BOULENGER, 1884: 220. — MNHN 1884.254, adult female (SVL 70.5 mm) and 1884.256, adult male (SVL 70.5 mm), same collection data as the lectotype.

NOTE ON PARALECTOTYPES. — Both paralectotypes studied are similar in size and colour to the lectotype. Other paralectotypes will certainly be found in the future in other Museums, as BOULENGER (1884) described this species using a series of 85 syntypes.

DIAGNOSIS

A large-sized green frog. Webbing of foot more important than in *Rana perezi* and *Rana* kl. *grafi*. Head larger than in these two taxons, tympanum-eye distance larger than half of tympanum diameter, vomerine teeth position intermediate.

DESCRIPTION OF LECTOTYPE OF *RANA FORTIS* BOULENGER, 1884

Slightly dried alcohol fixed specimen, snout-vent length 71.4 mm. Head longer (28.3 mm) than broad (26.0 mm); snout rounded, not protruding beyond mouth, longer (10.4 mm) than diameter of eye (7.6 mm); canthus rostralis rounded, loreal region abrupt, concave; interorbital space flat, smaller (2.3 mm) than both internarial distance (4.0 mm) and upper eyelid width (4.9 mm); nostril slightly nearer (5.5 mm) to eye than to tip of snout (5.3 mm); tympanum present, its diameter (5.3 mm) more than half of diameter of eye, its distance to eye (2.9 mm) roughly one half of its diameter; vestige of pineal eye absent, tongue ovally elongated, deeply emarginated behind, finely granulated. Vomerine teeth between choanae in two ridges forming an angle of 130°; ridges long (1.59 mm), 4.9 times the separation between them (0.34 mm).

Arm short, forearm (16.3 mm) shorter than hand (18.4 mm); finger length, shortest to longest: I = II < IV < III; length of third finger 9.9 mm; tips of fingers pointed; metacarpal tubercles not distinct, subarticular tubercles rounded, moderately developed.

Hind limbs relatively short, shank four times longer (36.1 mm) than broad (8.3 mm), longer than thigh (29.6 mm); shank and thigh both shorter than distance from base of inner metatarsal tubercle to tip of toe IV (41.2 mm); toes moderately long, length of IV (24.0 mm) more than one third of length from base of tarsus to tip of toe IV (56.2 mm); tips of toes pointed; webbing moderately developed (I 1/2 – 1 1/2 II 1/2 – 2 III 1 – 2 IV 2 – 1/2 V); inner metatarsal tubercle moderately developed, its length (3.4 mm) 3.4 times in length of toe I (11.6 mm); glandular ridge on tarsus flat.

Dorsum with large flat warts, except on top of head; two broad glandular dorsolateral ridges; ventral surfaces smooth.

Colour in alcohol: Grayish with few large darker spots; a slightly clearer mediodorsal line; dorsolateral folds slightly clearer; forelimbs with few darker spots; hind limbs with darker bands; ventral surface whitish marbled with black, very homogeneous; back of thigh blackish with few clearer spots. Vocal sacs blackish, nuptial pads on finger I blackish.

TABLE III. — Some morphometric ratios of type-specimens, allowing comparison with electrophoretically studied material. Values followed by an asterisk * fall outside the range of variation for the taxon given in Table II. (–): measurement not possible due to injuries. H: holotype; L: lectotype; PL: paralectotype.

Quelques rapports morphométriques chez quelques spécimens-types, permettant une comparaison avec les spécimens étudiés par électrophorèse. Les valeurs suivies d'un astérisque tombent en dehors de l'intervalle de variation donné pour le taxon dans le tableau II. (–): mensuration impossible en raison de blessures. H: holotype; L: lectotype; PL: paralectotype.

	Rana perezi		*Rana* kl. *grafi*	*Rana fortis*		
Ratio	MCZ 6832 L (adult ♀)	MNHN 1889.596 PL (adult ♀)	MNHN 1993.3374 H (adult ♀)	MNHN 1884.255 L (adult ♂)	MNHN 1884.254 PL (adult ♀)	MNHN 1884.256 PL (adult ♂)
FOTL / SVL	0.511	0.502	0.481	0.577	0.580	–
HW / SVL	0.343	0.351	0.332	0.364	0.363	0.369
IBE / SVL	0.218	0.234	0.179	0.200	0.217	0.203
IC / SVL	0.0933*	0.0909*	0.0712	0.0862*	0.101	0.0938
IMT / SVL	0.0591	0.0643	0.0478	0.0476	0.0511	0.0440
IN / SVL	0.0622*	0.0573	0.0460	0.0672	0.0644	0.0634
IV / IC	0.0997	0.0923	0.0127	0.0612	0.0436*	0.0470
IV / SVL	0.0093	0.0084	0.00097	0.0052	0.0044	0.044
IV / VRL	0.073	0.231	0.0282	0.183	0.127	0.172
THL / SVL	0.446	0.464	0.467	0.458	0.507	0.507
TL / SVL	0.459	0.464	0.459	0.505*	0.504*	0.509*
TYD / IN	1.225*	1.342*	1.373	1.104	1.171	1.073
TYD / SVL	0.0762*	0.0769*	0.0681	0.0754	0.0754*	0.0680
TYD / TYE	2.882*	2.75*	1.353	1.822	1.907	1.762
TYE / SVL	0.0264*	0.0280*	0.0331	0.0409	0.0395	0.0386
VRL / IC	0.367	0.379	0.482	0.296*	0.345	0.273*
VRL / SVL	0.0342	0.0344	0.0568	0.0253*	0.0349	0.0256*
WOFF / SVL	0.311	0.305	0.331	0.377	0.392	0.369
WOTF / FOTL	0.598	0.618	0.674	0.695	0.691	0.667
WOTF / SVL	0.306	0.311	0.324	0.389	0.401	0.380
WOTF / WOFF	0.984	1.020	0.979	1.032	1.018	1.030

DISCUSSION

Morphological distinction between *Rana perezi* and *Rana* kl. *grafi*

In our view, one of the goals of contemporaneous systematists should be to reconcile modern and traditional methods of biology to ensure continuity in science. Studies of genotypes allow understanding of genetic mechanisms involved in the evolution of taxa. But such methods cannot be used without heavy investigations and should be paired with study of external characters and morphology. On the basis of studies linking morphological and genetic information, keys based on purely morphometrical characters can be worked out. Such keys are necessary for work on collection material, field work, and preparation of distribution maps. Until now, most information collected in the past by ancient authors on the distribution of green frogs is obsolete, as the level of determination depended on the worker. To prepare well-founded keys would permit to go further in our knowledge about biogeography and evolution of green frogs.

The morphologies of *Rana perezi* and *Rana* kl. *grafi* had not been compared until now. This paper is a first step in this respect. Even if the sample is small, clear (significant) morphometrical differences were found between two electrophoretically determined groups of frogs. These characters permit identification of frogs for which no electrophoretic data are available.

The morphometric ratios traditionally used for species identification in the complex *lessonae – esculenta – ridibunda* do not work in the complex *perezi – grafi – ridibunda*. In the latter complex, the differentiation is more important in foot and vomerine teeth morphologies than in tibia, inner metatarsal tubercle, and inner toe lengths. This shows clearly that morphological studies should not only include characters that were valid for certain groups of species ("good" characters), but that the analysis should embrace the whole morphology, including measurements that concern all parts of the body.

Because of the small number of electrophoretically determined specimens available, in this study we pooled specimens from different populations, of the two sexes and of various ages and sizes. We excluded young specimens, because usually in frogs morphological changes are very important during ontogeny, mostly as a result of allometric growth. In the future, it will be interesting to investigate about variation between different populations and to include more taxa for comparison. But, to correctly study such a problem, close attention should be paid to the important intrapopulational variations in frogs due to sexual dimorphism and allometric growth.

In some of the studied ratios, *Rana* kl. *grafi* is intermediate between the two non-hybrid species. This might be a consequence of the hybrid origin of the klepton. In other ratios, *Rana* kl. *grafi* shows distinct new characters. Vomerine teeth position is not like in any of the two non-hybrid species, nor is it intermediate. It is clearly a new character.

Nomenclatural problems

A major aim of this study was to solve nomenclatural problems concerning green frogs from Southern France and Iberian Peninsula using the most parsimonious way. In a first step we defined morphometrical differences between the two taxa occurring there. Then we used these characters for phenotypical determination of the lectotype and one paralectotype of *Rana*

esculenta perezi Seoane, 1885: this study confirmed that both specimens are members of the non-hybrid taxon. This determination is consistent with the fact that only non-hybrid specimens have been found in Western Spain until now (UZZELL & TUNNER, 1983; ARANO *et al.*, 1995). This solves the first nomenclatural problem. The second is solved by the proposal in this paper of a new scientific name, *Rana* kl. *grafi*, for the klepton found associated with *Rana perezi* in some areas.

HISTORICAL CONSIDERATIONS

European green frogs seem to be a monophyletic group closely related to East Asian green frogs (UZZELL, 1982), with which they constitute the subgenus *Pelophylax* (DUBOIS, 1992). Within the Western green frogs, *Rana perezi* and *Rana saharica* seem to form a monophyletic group (UZZELL, 1982; BEERLI, 1993). This group probably was isolated on the African continent when the Mediterranean Sea was formed. Immigration to the Iberian Peninsula was made possible by the closing of the Straits of Gibraltar. Estimated divergence time between *Rana perezi* and *Rana saharica* corresponds to the date of reopening of the Straits of Gibraltar (BEERLI, 1993).

Currently, the Northern half of France is occupied by the L-E system (UZZELL & BERGER, 1975), *i.e.* mixed populations of *Rana lessonae* and *Rana* kl. *esculenta*, while the southern part of the country is occupied by the P-RP system (GRAF & POLLS PELAZ, 1989) or P-G system, *i.e.* mixed populations of *Rana perezi* and *Rana* kl. *grafi*. Besides, there is evidence of occurrence of isolated populations of *Rana ridibunda* in various parts in France (CASTANET & GUYÉTANT, 1989; CROCHET, DUBOIS & OHLER, unpubl.). The origin of the latter frogs is unknown: some populations (near universities, etc.) are probably introduced (see *e.g.* DUBOIS, 1982), while others are so isolated that such an origin seems unlikely. These frogs have not yet been compared with *Rana ridibunda* of Central and Northern Europe.

Rana perezi seems to have been a rather recent invader of Europe coming from the South. During its expansion it may have come in contact with the more Northern and Eastern European taxa, possibly in Southern France. *Rana* kl. *grafi* would have appeared through hybridization in this contact zone. There may have been primarily direct contact between *Rana perezi* and *Rana ridibunda*, or the *ridibunda* genome may have been transmitted from *esculenta* to *grafi* through hybridization between *perezi* and *esculenta* (DUBOIS & GÜNTHER, 1982: 296).

Other hypotheses can be considered. As the estimated age of European green frogs is much older than the estimated age of immigration of the *perezi-saharica* stock into the Iberian Peninsula, there might have existed a pre-*perezi* frog in South-Western Europe. This might have been the L-E system, progressively replaced by the P-G system, with a contact/hybrid zone that would move northwards with progression of the latter. This would require competitive superiority of the P-G system over the L-E system in this area, which could be experimentally tested. A detailed study of the composition, structure and dynamics of green frog populations in areas where the P-G system probably meets the L-E system (*e.g.* Charente in Western France, Rhône valley, Southern Massif central) might also throw interesting lights on this question. Another hypothesis would be that a *ridibunda*-like species might have been replaced in the Iberian Peninsula by the P-G system. Some of the morphometrical particularities of *grafi* might indicate that the second parental species was somewhat different from the current European *ridibunda*.

Acknowledgements

We warmly thank the following colleagues for the help they provided for this work: Jean-Daniel GRAF (Genève) deposited some of his electrophoretically determined specimens in the Paris Museum collections; Leszek BERGER (Poznan) gave a large collection of Polish frogs to the Paris Museum; Jose P. ROSADO (Harvard, Cambridge) sent us in loan the syntype of *Rana esculenta perezi* kept in the collections of the Museum of Comparative Zoology; Roger BOUR (Paris) provided helpful comments and suggestions; Laurent BESSOL (Paris) kindly prepared the macrophotographs of Fig. 1.

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First record of the genus *Candelabrum* (Cnidaria, Hydrozoa, Athecata) from the Mid-Atlantic Ridge: a description of a new species and a review of the genus

by Michel SEGONZAC and Willem VERVOORT

Abstract. — Two species of *Candelabrum* (Cnidaria, Hydrozoa, Athecata) have been discovered and collected at two hydrothermal areas of the Mid-Atlantic Ridge with French and American submersibles during five cruises in 1988, 1993 and 1994. The first, *Candelabrum serpentarii* nov. sp., has been found at the Snake Pit site (23°N, 3500 m depth) and represents an undescribed species. The second, *Candelabrum phrygium* (Fabricius, 1780), collected at the Lucky Strike site (37°N, 1700 m depth), is known to have a circumarctic distribution. In spite of great differences in depth of occurrence, considerable morphological similarities exist between the new species and the intertidal species *C. cocksii* (Vigurs, 1849). This discovery has given rise to a review of the genus *Candelabrum*. In addition, ecological remarks on these three species are presented.

Keywords. — Hydrothermal vents, Mid-Atlantic Ridge, Hydrozoa, *Candelabrum*, biogeography, plate tectonics.

Premières observations du genre *Candelabrum* (Cnidaria, Hydrozoa, Athecata) sur des zones hydrothermales de la dorsale médio-atlantique : description d'une nouvelle espèce et revue du genre

Résumé. — Deux espèces de *Candelabrum* (Cnidaria, Hydrozoa, Athecata) ont été découvertes et récoltées sur deux aires hydrothermales de la dorsale médio-atlantique grâce aux sous-marins français et américains au cours de cinq missions en 1988, 1993 et 1994. La première, *Candelabrum serpentarii* nov. sp., récoltée sur le site du Snake Pit (23° N, 3500 m), est une espèce non décrite. La seconde, *Candelabrum phrygium* (Fabricius, 1780), récoltée sur le site Lucky Strike (37° N, 1700 m), est connue pour sa répartition circumarctique. En dépit des différences de profondeur des habitats, on remarque de fortes ressemblances morphologiques entre l'espèce non décrite et l'espèce littorale connue *C. cocksii*. Ces découvertes donnent lieu à une revue des espèces du genre *Candelabrum*. Quelques remarques écologiques sur ces trois espèces sont présentées.

Mots-clés. — Sources hydrothermales, dorsale médio-atlantique, Hydrozoaire, *Candelabrum*, biogéographie, tectonique des plaques.

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INTRODUCTION

The first Atlantic hydrothermal communities found in the axial valley of the Mid-Atlantic Ridge: the TAG (Trans-Atlantic Geotraverse) area at 26°N (Fig. 1) and 3700 m depth, and the Snake Pit area at 23°N and 3500 m depth, have been described respectively by GALKIN *et al.* (1990) and SEGONZAC (1992). At the Snake Pit area, an undescribed species of *Candelabrum*

was collected by the submersible *Nautile* during the French cruise Hydrosnake in June 1988 and several other specimens were seen next to the active edifices. In June 1993, another specimen was collected at the same site with the submersible *Alvin* during the American-French cruise MAR 93. *In situ*, this organism, belonging to the class Hydrozoa, appeared as a whitish gelatinous pen, undulating according to the water movements. Fixed on pillow lava or sulfide rock, it is about 10 cm long and presents, on its base, pure white, clustered granulations (gonophores). It was the first time that such organism, known from shallower waters, had been observed among the hydrothermal communities.

Sampling of the hydrothermal fauna of the newly found Lucky Strike area (SW Azores Islands, 37°N, 1700 m depth), realized in May 1993 with the submersible *Alvin* (LANGMUIR *et al.*, 1993), allowed the collection of another species of hydroid, known as *Candelabrum phrygium* (FABRICIUS, 1780), among a sample of the mussel *Bathymodiolus* sp. During the French cruise Diva 2 (June 1994), several other specimens were observed and collected at the same location with the submersible *Nautile*.

In the Hydroida (hydropolyps-hydromedusae) of the Hydrozoa, the subclass Athecatae (Anthomedusae) is principally characterized by the absence of a distinct hydrotheca around the polyp. It comprises c. 50 families that are mostly marine. Among these families, the Candelabridae has only two genera: *Candelabrum* de Blainville, 1830, and *Monocoryne* Broch, 1910; *Candelabrum* has 14 species. The species of *Candelabrum* discovered at the Snake Pit is described here. It presents surprising morphological resemblances with the species *Candelabrum cocksii* (VIGURS,

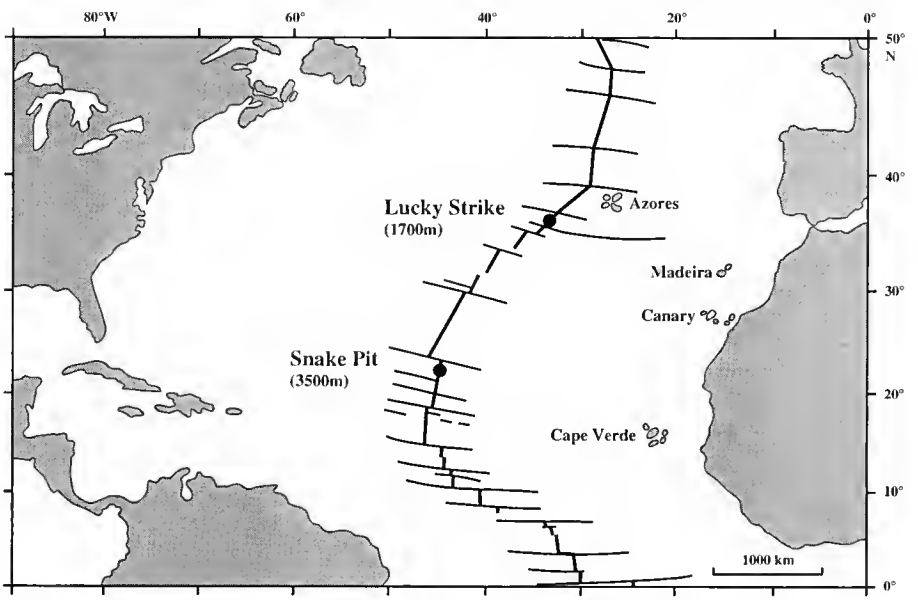


FIG. 1. — Map of the northern Atlantic showing the position of the Mid-Atlantic Ridge and hydrothermal sites Snake Pit (locality for *Candelabrum serpentarii* nov. sp.) and Lucky Strike [locality for *Candelabrum phrygium* (FABRICIUS, 1780)].

Carte de l'Atlantique Nord indiquant la position de la dorsale médio-atlantique et des sites hydrothermaux du Snake Pit (localité de Candelabrum serpentarii *nov. sp.) et de Lucky Strike [(localité de* Candelabrum phrygium *(FABRICIUS, 1780)].*

1849), well known from intertidal areas. The species *Candelabrum phrygium* (FABRICIUS, 1780), collected at Lucky Strike, is known to have a circumarctic distribution. These new data prompted us to review the genus, while in the course of our investigation it became imperative to compare the specimens from the Mid-Atlantic Ridge with the intertidal species. Ecological observations were added where appropriate.

Discussion of the trophic behaviour and hypothesis about the distribution of these two hydrothermal species on active sites are presented.

MATERIAL

Specimens of *Candelabrum serpentarii* nov. sp. were obtained from the Snake Pit hydrothermal vents area (Mid-Atlantic Ridge, 23°23'N-47°56'W, 3500 m depth), first during the French cruise Hydrosnake, submersible *Nautile*/N. O. *Nadir*, June 12-July 14, 1988, chief scientist: Catherine MÉVEL (Université Paris-VI); second by American cruise MAR 93, submersible *Alvin*/R. V. *Atlantis II* and J. *Charcot*, June 5-30, 1993, chief scientists: Cindy VAN DOVER (WHOI) and Aline FIALA (Université Paris-VI). The photograph of that species (Fig. 3A) originates from the same locality and was provided by the French cruise Gravinaut, *Nautile*/N.O. *Nadir*, September 7-October 4, 1993, chief scientist: Jacques DUBOIS (Institut de Physique du Globe, Paris).

The specimens of *Candelabrum phrygium* were obtained from the Lucky Strike hydrothermal vents area (Mid-Atlantic Ridge, 37°17'N-32°16'W, 1626-1700 m depth), first by the American cruise Lucky Strike, *Alvin*/R. V. *Atlantis II*, May 27-June 4, 1993, chief scientist: Charlie LANGMUIR (Lamont-Doherty Earth Observatory); second by the French cruise Diva 2, *Nautile*/N.O. *Nadir*, June 2-July 4, 1994, chief scientists: Daniel DESBRUYÈRES and Anne-Marie ALAYSE (IFREMER).

In addition, both species and their environment were observed *in situ*, on videotape and on photographs taken by the submersible *Nautile*.

Some specimens of *Candelabrum cocksii* were placed at our disposal by Dr A. CASTRIC-FEY (Collège de France, Concarneau) and came from her private collection. Specimens of *Candelabrum phrygium* and some of the other species of *Candelabrum* were studied by one of us (W. V.) in the collections of The Natural History Museum, London.

REVIEW OF THE GENUS

CANDELABRUM de Blainville, 1830

Candelabrum de Blainville, 1830: 284; type, by monotypy: *Lucernaria phrygia* Fabricius, 1780 (= *Arum* Vigurs, 1849: 90, type, by monotypy: *Arum Cocksii* Vigurs, 1849; *Myriothela* M. Sars, 1851: 126, type, by monotypy: *Myriothela arctica* M. Sars, 1851; *Spadix* Gosse, 1853b: 125, type, by monotypy: *Spadix purpurea* Gosse, 1853b; *Acandela* Stechow, 1920: 45, type, by monotypy and original designation: *Myriothela mitra* Bonnevie, 1898).

DESCRIPTION

Solitary hydroids of worm-like appearance; length varied, between 10 and 300 mm total body length. Body divisible into three regions: a basal region (foot, hydrorhiza) serving attachment of the specimen, a blastostyle bearing region and a distal body portion, usually tapering, having a small, circular mouth at its extreme end. Shape and development of foot differing in the various species and with age: flattened and lobed to a varied extent or root-shaped, being in that case a conical, pointed part of the body. Attaching filaments occur on both lobed and root-shaped types of foot, usually with chitinous discs for attachment to solid substrates. Whole or part of foot in some species with chitinous sheath, also including the attaching discs and occasionally of considerable thickness. Blastostyle region only distinguishable in sexually mature individuals, usually swollen compared to distal part of body; blastostyles are tubular to conical prolongation of the body wall bearing male and/or female cryptomedusoid gonophores; body cavity may continue in blastostyle; these arranged in one or several whorls or irregularly distributed. Dioecious, but in *C. cocksii* and *C. serpentarii* nov. sp. monoecious with hermaphroditic blastostyles. Development of larva to actinula in female gonophore, one or more may be present. Feeding tentacles (claspers) attaching to gonophore with developing egg described for one species (*C. cocksii*), may also be present on others. Distal part of body (trunk) as long as or much longer than blastostyle bearing region, usually set with numerous small, capitate tentacles. Occasionally tentacles continue downwards into the blastostyle bearing region and/or occur on the blastostyles. Some species have modified tentacles on blastostyle or foot. Enteron with folds of endoderm. Cnidome composed of (usually two types of) desmonemes, haplonemes (probably atrichous), heteronemes and stenoteles.

REMARKS

The type species was considered by FABRICIUS (1780) to be a species of stalked jellyfishes (Stauromedusae) and described as *Lucernaria phrygia*. DE BLAINVILLE (1830, 1834) placed it near the genus *Sipunculus*, now in the phylum Sipunculida, instituting for its reception the genus *Candelabrum*. M. SARS (1851) redescribed the species as *Myriothela arctica;* in 1857, M. SARS reported on the rediscovery of some of FABRICIUS's material in Copenhagen and referred FABRICIUS's species to *Myriothela*, this generic name being preferred by M. SARS (1871) and ALLMAN (1874). L. AGASSIZ (1860-1862) regarded *Candelabrum* de Blainville, 1830 and *Myriothela* M. Sars, 1851, as being congeneric, and also recognized *Candelabrum* as the oldest available name. The genus name *Arum* was used by VIGURS (1849) for his species *Arum Cocksii*, later on redescribed by GOSSE (1853b) as *Spadix purpurea*. *Spadix* Gosse, 1853(b) thus is a junior subjective synonym of *Arum* Vigurs, 1849. There are only two main characteristics separating *Arum* from the species of *Candelabrum (cf.* STECHOW, 1922: 144; 1923: 38): the development of the foot and the presence of claspers. The morphology of the foot in several species of *Myriothela* (= *Candelabrum*) has been studied by MANTON (1940). It seems clear that a foot surrounded by a continuous and conspicuous sheath of chitinous periderm begins with the development of such perisarc surrounding the place of contact between modified tentacles and the substrate, the tentacles being in many instances lobed extrusions of the foot (our observations). The chitinous perisarc, at least in *C. cocksii*, may ultimately fuse to form a continuous sheath

covering the foot, thinning out distally and merging with the thin cuticle covering the ectoderm. It thus appears that the morphology of the foot is dependent upon the age of the specimen and most likely also on the substrate and considering the limited number of species that has adequately been studied, in this respect it is, in our opinion, unsuitable for generic distinction. The use of the generic name *Candelabrum* has recently been reintroduced by HAND & GUILLIAM (1951), PREVOT (1959) and CORNELIUS (1977).

C. cocksii so far is the only species in which the presence of claspers has been established; they definitely seem to be absent from *Candelabrum phrygium*, the only remaining species in *Candelabrum* of which the life history has to some extent been studied. All other species (with the exception of course of *C. cocksii*) have been studied from preserved material. The presence of claspers, considered by MANTON (1940) to represent modified tentacles (for attachment) cannot altogether be excluded in such insufficiently known species of *Candelabrum*. It seems illogical to separate *Arum* from *Candelabrum* on the morphology of the foot, which is dependent upon development and substrate, and the presence or absence of claspers, a character which cannot be properly evaluated in all species of *Arum* and *Candelabrum*. We have therefore sunk *Arum* Vigurs, 1849, into the synonymy of *Candelabrum* de Blainville, 1830, the latter having priority. We thus follow CORNELIUS (1977) in referring *Arum*, *Myriothela* and *Spadix* to *Candelabrum*.

The genus *Acandela* Stechow, 1920, was instituted by STECHOW for *Myriothela mitra* Bonnevie, 1898, the only diagnostic character being the absence of (clavate) tentacles on the distal portion of the body. BONNEVIE's *Myriothela mitra* may be based on a single specimen (the number is not stated in the description), moreover it was obtained from deep water (2220 m), so it probably had a rough assent in a trawl net. The possibility that the specimen consequently was damaged, resulting in the loss of tentacles, cannot be excluded and has in fact been described in other species of *Candelabrum* (*e.g. C. austrogeorgiae*). We have relegated *Acandela* to the synonymy of *Candelabrum*.

REVIEW OF THE SPECIES AND DESCRIPTIONS

Candelabrum arcticum (M. Sars, 1851)

Myriothela arctica M. Sars, 1851: 126, 131, 134 [= *Candelabrum phrygium*[1] (Fabricius, 1780)].

Candelabrum australe (Briggs, 1928)

Myriothela australis Briggs, 1928: 307-312, Pl. 32, Pl. 33 Fig. 3, Pl. 34 Figs 1-4: BRIGGS, 1929: 244-264, Figs 1-4, Pls 42-44; BRIGGS, 1939: 10; MANTON, 1940: 280 et seq., Fig. 8a; DAKIN, BENNETT & POPE, 1948: 208; RALPH, 1966: 158, 162.

Candelabrum australe — HAND & GWILLIAM, 1951: 208.

LOCALITY. — Found "on the lobes of the thallus of a seaweed thrown up on the sandy beach of Maroubra Bay near Sydney, N. S. W." (BRIGGS, 1928).

1. See discussion of synonymy of this species.

REMARKS

Description and studies on gonophore development based on forty specimens from the locality given above; no accurate depth record of the living specimens is given. Length ranging from 4 to 30 mm, body elongated, basally cylindrical; blastostyle bearing region narrowed, "marked by a series of well defined longitudinal furrows with finer transverse striations". Distal portion of body, above blastostyle region, covered by capitate tentacles. Blastostyles close together, abundant, unbranched, elongate, cylindrical and clavate at distal extremity, there bearing a bundle of tentacles differing from those on body by trumpet-shaped head and larger size, having a long, slender, cylindrical stem. Male and female blastostyles on separate individuals (dioecious). Female blastostyle with 3-4 mature and 6-8 immature gonophores on proximal portion; apex with 8-10 tentacles. Male blastostyles smaller and more numerous, some 15 being present; apex with 6-9 tentacles. "Male and female gonophores have an apical opening representing the velar aperture. The proximal end of the hydranth is truncated and is attached to the substrate by a number of tentacle-like filaments which constitute the hydrorhiza. At the truncated end of each of these short rooting processes is a small, circular, chitinous disc of dark brown colour" (BRIGGS, 1928). There are no claspers. Additional specimens from Port Phillip Bay, near Melbourne, Australia, are mentioned by RALPH (1966); length of preserved specimens 20-35 mm.

Candelabrum austrogeorgiae (Jäderholm, 1904)

Myriothela austro-georgiae Jäderholm, 1904: ii; JÄDERHOLM, 1905: 4, 6-9, 38, Pls 1-2, Pl. 3 Figs 1-3; BILLARD, 1906: 2, 4-9, Figs 1-3; HICKSON & GRAVELY, 1907: 19; RITCHIE, 1909: 67, 69-70; STECHOW, 1909: 37, 66; VANHÖFFEN, 1910: 272, 277, 339; BRIGGS, 1928: 315, 1939: 10; MANTON, 1940: 281, 282; REES & THURSFIELD, 1965: 45; STEPAN'YANTS, 1972: 63-64, Fig. 9, 1979: 27, Pl. 5 Fig. 5, Pl. 25 Fig. 2.

Candelabrum austrogeorgiae — STECHOW, 1922: 144; STECHOW, 1923: 45; HAND & GWILLIAM, 1951: 208.

Gonostyle of Siphonophore, THOMPSON, 1904: 19, Pl. 1.

LOCALITIES. — "Vor Cumberland, Sth Georgia, 252-310 m, 5. vi. 1902; Stn 81, Bransfield Strait, 849 m, 25. xi. 1902; Stn 90, Bransfield Strait, 719-726 m, 05. xii. 1902" (JÄDERHOLM, 1905).

Flanders Bay, Graham Land, 15. ii. 1904; Booth-Wandell Island, 26/30. ix and 28. x. 1904, low tide (BILLARD, 1906).

"Scotia Bay in the South Orkneys, 10 fms, iv. 1903; 9-10 fms, v. 1903; among mud and pebbles, 18. xii. 1903". "On surface of the water, in a hole which had been cut in the ice. The depth of the water at that place was 20-30 fathoms, the temperature was 29° F" (RITCHIE, 1909).

"Observatory Bay, Kerguelen, 05. i. 1902, 10 × 4 mm" (VANHÖFFEN, 1910).

Davis Sea, Antarctica, near station Mir, 15-18 m; panantarctic species (STEPAN'YANTS, 1979).

REMARKS

Original description, by JÄDERHOLM (1904, 1905), based on unknown number of specimens from South Georgia. Body worm-like, up to 300 mm long, composed of foot, blastostyle bearing region and distal part exclusively bearing tentacles. Foot up to 20 mm long, basally with 3-4 mm long projections bearing filaments for attachment, flattened at the tip. There is no perisarc. Blastostyle bearing region c. half length of distal region, with blastostyles and capitate tentacles.

Blastostyles slender, tubular, with a single terminal tentacle or a number of smaller tentacles, bearing male or female gonophores; species is dioecious. Female gonophores usually 1-3, occasionally up to 6; male gonophores up to 10, of smaller diameter. Blastostyle bearing region not wider than remaining, distal part of body, which tapers gradually and is covered by numerous small capitate tentacles without noticeable arrangement.

The nematocysts are described to some extent by BILLARD (1906), who distinguishes two types, viz. stenoteles and desmonemes; no measurements are given. Some additional morphological details are given in the description of RITCHIE (1909) of specimens from the South Orkneys; on these specimens THOMPSON's (1904) description of the gonostyle of an unknown giant Siphonophore is based, placed by RITCHIE in the synonymy of the present species. The species is also redescribed by STEPAN'YANTS (1972, 1979).

Candelabrum capensis (Manton, 1940)

Myriothela capensis Manton, 1940: 276-287, Figs 7, 8b, 9, Pl. 1 Figs 12, 13, Pl. 3 Fig. 27; MILLARD, 1957: 186, 1966: 437; DAY, FIELD & PENRITH, 1970: 12; BOUILLON, 1974: 143; MILLARD, 1975: 45, Figs 7D, 18A, F, G, 1978: 195 et seq., 1980: 130.

Candelabrum capensis — PREVOT, 1959: 98.

LOCALITIES. — "Aquarium Rocks, East London, Sth Africa, 17 & 19. vii. 1937, 8-17 m" (MANTON, 1940). False Bay, 34° 08.5' S-18° 34.5' E, 27 m, female specimen, 6.5 mm (MILLARD, 1957).

West coast Cape Peninsula, Kommetje, 34° 08.5' S-18° 19.4' E, almost mature male attached to weed. Ludertitz Bay, South-West Africa, 26° 38' S-15° 09.3' E, two mature male specimens and two young specimens attached to crustacean appendage, largest 16 mm. Lamberts Bay, West coast Cape Peninsula, 32° 04.7' S-18° 18.2' E, 17 m, mature female specimen attached to weed (MILLARD, 1966). According to MILLARD (1975) maximum body length c. 25 mm.

REMARKS

Body c. 25 mm long, cylindrical, slowly tapering from base onward; basal portion (foot) c. one tenth of body length, attached, usually to algae, by means of 20-30 adhesive processes capped by chitinoid discs (MILLARD, 1975: 45). Blastostyles up to 4 mm long in single whorl of c. 20 above foot; unbranched, up to nine gonophores in proximal region and 4-7 capitate tentacles in distal region; species dioecious. Female gonophores releasing up to three actinulae. Distal part of body bearing many (400-600) densely packed, capitate tentacles. Cnidome adequately described by MILLARD (1966, 1975), composed of desmonemes (7.8-16.8 × 5.5-12.6 μm), stenoteles (9.9-11.4 × 7.2-8.1 μm), heteronemes (11.7-19.2 × 3.6-6.0 μm), haplonemes (10.8 × 9.9 μm) and probably also atrichous isorhizas (18.0 × 6.0 μm).

Candelabrum cocksii (Vigurs, 1849)
(Fig. 2c-d, Table 1)

Arum Cocksii Vigurs, 1849: 90.

Arum Cocksi(i) — COCKS, 1849: 90, 1852: 22, 1853a: 34, Pl. 3 Figs 7-12; M. SARS, 1857: 195; STECHOW, 1922: 144; REES, 1956: 116; Marine Biological Association of the United Kingdom, 1957: 39; REES, 1957: 487, Fig. 39A, B; PREVOT, 1959: 97, Pl. 1 Fig. 1; BRUCE, COLMAN

& JONES, 1963: 48; TEISSIER, 1965: 11; VAN DE VYVER, 1968: 349, Figs 16, IV, V; FEY, 1970: 390; CASTRIC-FEY, 1970: 20; CORNELIUS, 1977: 521 et seq; VAN DE VYVER, 1980: 110, 112; CASTRIC & MICHEL, 1982: 79, Fig.

Spadix purpurea Gosse, 1853b: 126-127; COCKS, 1853b: 365.

Spadix purpurea p.p. FORBES, 1854: 31 (excl. synonyms).

Spadix cocksii — GOSSE, 1853b: 386: M. SARS, 1857: 195; G. O. SARS, 1877: 28, note.

Myriothela cocksi(i) — G. O. SARS, 1874: 96, 130, 135; HINCKS, 1874: 136, 137; STORM, 1882: 7, 28, 30, at least part of specimens belong to *Monocoryne gigantea* (BONNEVIE, 1898, fide SWENANDER, 1904); PENNINGTON, 1885: 58, Pl. 3 Fig. 4; BONNEVIE, 1899: 9, 31-34, 37; SWENANDER, 1904: 4, 6; JÄDERHOLM, 1905: 8; BILLARD, 1906: 5, 9; BROCH, 1910: 194, 233, 238; BEDOT, 1911: 212; BILLARD, 1912: 460, 1921: 12-17, Fig. 1; BENOÎT, 1923a: 1836-1838, 1923c: 507-510, Figs 1-4; PRENANT & TEISSIER, 1924: 26; BENOÎT, 1925: 89 et seq., 113-193, Figs 1-35; CHADWICK, 1926: 51; WEILL, 1926: 1244 et seq.; BILLARD, 1927: 513-514; Marine biological Association of the United Kingdom, 1931: 69; WEILL, 1934a, b: 44, 106, 124, 125, 355, 373-375, 444, Figs 114-116; MOORE, 1937: 40; BRUCE, 1939: 12; EALES, 1939: 38, Pl. 3 Fig. 8; PÉRÈS, 1939: 539, Pl. 25 Fig. 1; BASSINDALE, 1941: 147; MANTON, 1941: 143 et seq., Figs 1-2; BRUCE, 1948: 45; TEISSIER, 1950: 11; BARRETT & YONGE, 1958: 47, Pl. 1; EALES, 1961: 34, Pl. 3 Fig. 8, 1967: 34, Pl. 3 Fig. 8; HARVEY, 1969: 14; ROBINS, 1969: 329; NICHOLS, COOKE & WHITELEY, 1971: 9, Fig.; BOUILLON, 1974: 143; HISCOCK, 1974: 23; BEIGEL, 1976: 121, Fig. 1, Pls 1-4; BEIGEL-HEUWINKEL, 1982a: 225 et seq., 1982b: 199-210, Figs 1-22, 1984: 273, 1988: 57-66, Figs 1-12.

Candelabrum cocksi — KRAMP, 1938: 66; HAND & GWILLIAM, 1951: 208; CORNELIUS, 1977; CORNELIUS & RYLAND, 1990: 116, Fig. 4.6.

Myriothela arctica — WRIGHT, 1858: 433; WRIGHT, 1859: 108; HINCKS, 1861: 157-158; ALLMAN, 1864a: 411, 1864c: 63.

Myriothela arctica p.p. FORBES, 1854: 31 (excl. synonyms).

Candelabrum arcticum p.p. L. AGASSIZ, 1862: 341 (excl. synonyms).

Myriothela phrygia — HINCKS, 1868: 77, Pl. 12 Fig. 3 (excl. synonyms in part). [Not *Myriothela phrygia* (Fabricius, 1780)].

Myriothela phrygia — ALLMAN, 1874: 317-321, 1875a: 135; BOURNE, 1889: 5, 1890: 392; HARDY, 1891: 505 et seq., Pls 36-37; GARSTANG, 1894: 223; CRAWFORD, 1895: 259 (*Myriothela phrygia*); GAMBLE, 1896: 132; BROWNE, 1897: 243; PRUVOT, 1897: 584, Tab. 22; BLACKBURN, 1899: 58 et seq., Pl. 8; LABBÉ, 1899: 4 et seq., Pl. 1 Figs 1, 4-9, Pl. 2 Figs 13, 17, 21; BEAUMONT, 1900: 756, 766; BROWNE, 1904: 162, 188; HAECKEL, 1904: Pl. 6 Fig. 12; HARTLAUB, 1904: 100; BOULENGER, 1908: 360; MÜLLER, 1908: 73; BOULENGER, 1910: 775. [All not *Myriothela phrygia* (Fabricius, 1780)].

Myriothela phrygia p.p. ALLMAN, 1872: 168, 382 (excl. synonyms in part). [Not *Myriothela phrygia* (Fabricius, 1780)].

Myriothela — ALLMAN, 1875b: 250 et seq.; (De) KOROTNEFF, 1878: 363-365, 1879: 187-190.

Myriothela p.p. (De) KOROTNEV, 1880: 5-37, Figs 1-29, Pls 1-4.

Myriothèle — (De) KOROTNEFF, 1888: 21 et seq., Pls 1-2.

MATERIAL EXAMINED. — Three complete specimens and two damaged individuals from Glénan Islands, off the Atlantic coast of France, collected in 1964 and 1965, in the tidal zone and upper subtidal zone; depth up to 17 m.

DIAGNOSIS

Body composed of foot, blastostyle region and trunk. Foot large, only slightly shorter than blastostyle region, with a number of slender prolongations that attach body to substrate, basis of each prolongation with chitinous perisarcal disk; chitinous perisarc gradually extending upwards and covering whole foot, externally more or less spinous. Monoecious, blastostyles slender, with male and female gonophores and occasionally with some developing eggs attached by claspers; dispersed capitate tentacles also occur. There is no terminal circle of tentacles. Trunk in our specimens 15-20 mm long, collapsible, covered by small, capitate tentacles with ovoid to globular capitulum; nematocysts dispersed.

DESCRIPTION

The more noticeable difference with both *C. serpentarii* and *C. phrygium* is in the development of the foot, which in the present species represents a conspicuous part of the body, attached to the substrate by means of finger-shaped to lobed prolongations, that terminally have a distinct chitinous disk, by means of which the specimens are attached to the front of algae, to calcareous algae or to fragments of rock. The chitinous perisarc surrounding the attaching disks reaches upwards to cover the whole of the foot with a layer of yellowish-brown perisarc, externally rough to spinous. Development of this chitinous sheath is different in the various specimens. The region bearing the blastostyles is c. 8 mm long; the blastostyles number 5 to 8 and are long and thin, carrying male and female gonophores in various stages of development, the males vary in diameter between 0.30 and 0.42 mm; the ripe female gonophore (with ovum) measures 0.60 mm in diameter. In addition some of the blastostyles have a developing egg attached by means of one or several claspers, resembling tentacles with a disc-shaped apical portion attached to the hyaline egg membrane. Inside is a developing larva (actinula); diameter of whole structure c. 1 mm. The state of preservation of the material does not permit further, more detailed observation. The trunk portion of the body, in the present specimens, is 15-20 mm long, tube-shaped and quite weak, which may be largely the result of inadequate fixation followed by transportation of the specimens. No mouth could be found; the exterior of the trunk is covered with small, capitate tentacles, pedicel 200-250 µm long, capitulum (often elongated ovoid) 130-200 µm diameter. The nematocysts are dispersed over the exterior of the capitulum and have been studied in squash preparations. There are two size classes of desmonemes, as well as haplonemes and stenoteles. Large and small desmonemes are about equally abundant, ovoid and slightly asymmetrical because of the development of a slight elevation just besides the top of the capsule. Large desmonemes 13.8-14.0 × 8.8-9.1 µm; small desmonemes 6.5-8.5 × 4.5-4.9 µm. They contain a thick thread irregularly coiled inside capsule. Haplonemes present in small number, slenderer than in the other two species and more asymmetrical, occasionally slightly banana-shaped, 18.8-20.5 × 6.2-6.6 µm. The longitudinal portion of the thread is clearly visible but the obliquely transverse coils are difficult to see. Stenoteles found in considerable numbers, ovoid with flattened top, perfectly symmetrical, 9.8-10.7 × 8.2-8.6 µm; shaft visible with folded barbs inside.

REMARKS

The principal area of distribution of this species is in the intertidal zone of the English Channel coasts of Great Britain and France. It is definitely known to occur also at the Glénan

TABLE 1. — Synoptic table differentiating between three described species of *Candelabrum*

	C. cocksii	*C. phrygium*	*C. serpentarii*
Size	1-2 cm	4-40 cm	8-15 cm
Locality	Intertidal zone of NE Atlantic.	Circumarctic and at active hydrothermal vents in the NE Atlantic in water of c. 11° C loaded with sulfureous compounds.	Restricted to an area around hydrothermal vents in water of 2.4° C.
Food	Probably small Crustacea (Copepoda and Amphipoda).	Shrimps and small Crustacea (Amphipoda, Copepoda)	Probably Crustacea
Reproduction	Monoecious; claspers present; young polyp developing into actinula; dispersal consequently restricted.	Dioecious; no claspers observed; development of young polyp unknown.	Monoecious; no claspers observed; development of young polyp unknown.
Nematocysts*			
Desmonemes (in µm)	13.8-14.0 × 8.8-9.1 (large) 6.5-8.5 × 4.5-4.9 (small)	12.5-13.0 × 9.0-9.8 (large) 8.2-9.0 × 6.4 × 6.6 (small)	13.0-14.5 × 9.8-10.5 (large) small type not observed
Haplonemes (in µm)	18.8-20.5 × 6.2-6.6	19.7-20.5 × 8.2-9.9	16.5-18.0 × 7.8-8.2
Stenoteles (in µm)	9.8-10.7 × 8.2-8.6	10.6-11.5 × 8.2-9.8	9.8-11.5 × 9.5-10.5

* It should be borne in mind that all observations in the present material are based on observations of unexploded nematocysts; the identifications of the various types, particularly the haplonemes, are tentative.

Archipelago (where some individuals were observed in May 1994) in the northern Bay of Biscay, at the Scilly Islands, at the Isle of Man and in the Bristol Channel. The records from Norway (*e.g.* KRAMP's, 1938, record from "Norway S. of Lofoten") are exclusively based on G. O. SARS's remarks on the occurrence of this species in deep water (100-200 m) off Aalesund, Norway; there are no recent records from the Norwegian coast. However, one of us (W. V.) has seen an undubitable specimen in an intertidal collection from the Bay of Cadiz, Atlantic coast of southern Spain, made by Dr M. D. MEDEL, Huelva, Spain.

It is quite a problem to state accurately the geographical distribution of this, apparently not quite rare, intertidal species because of its frequent confusion with *Candelabrum phrygium*. Since 1874, the differences between both species have been pointedly worded by G. O. SARS; his publication in Norwegian apparently escaping the notice of many later scientists. The confusion resulting from the tangled synonymy of the two species unfortunately has been aggravated by CORNELIUS' 1977 paper, in which both species are considered conspecific and the fact is overlooked that REES (1956) was fully aware of their specific differences.

(De) KOROTNEV's (1880) lengthy Russian description of *Myriothela* refers partly to *Candelabrum cocksii* which he studied at Roscoff; many details and some of the drawings have

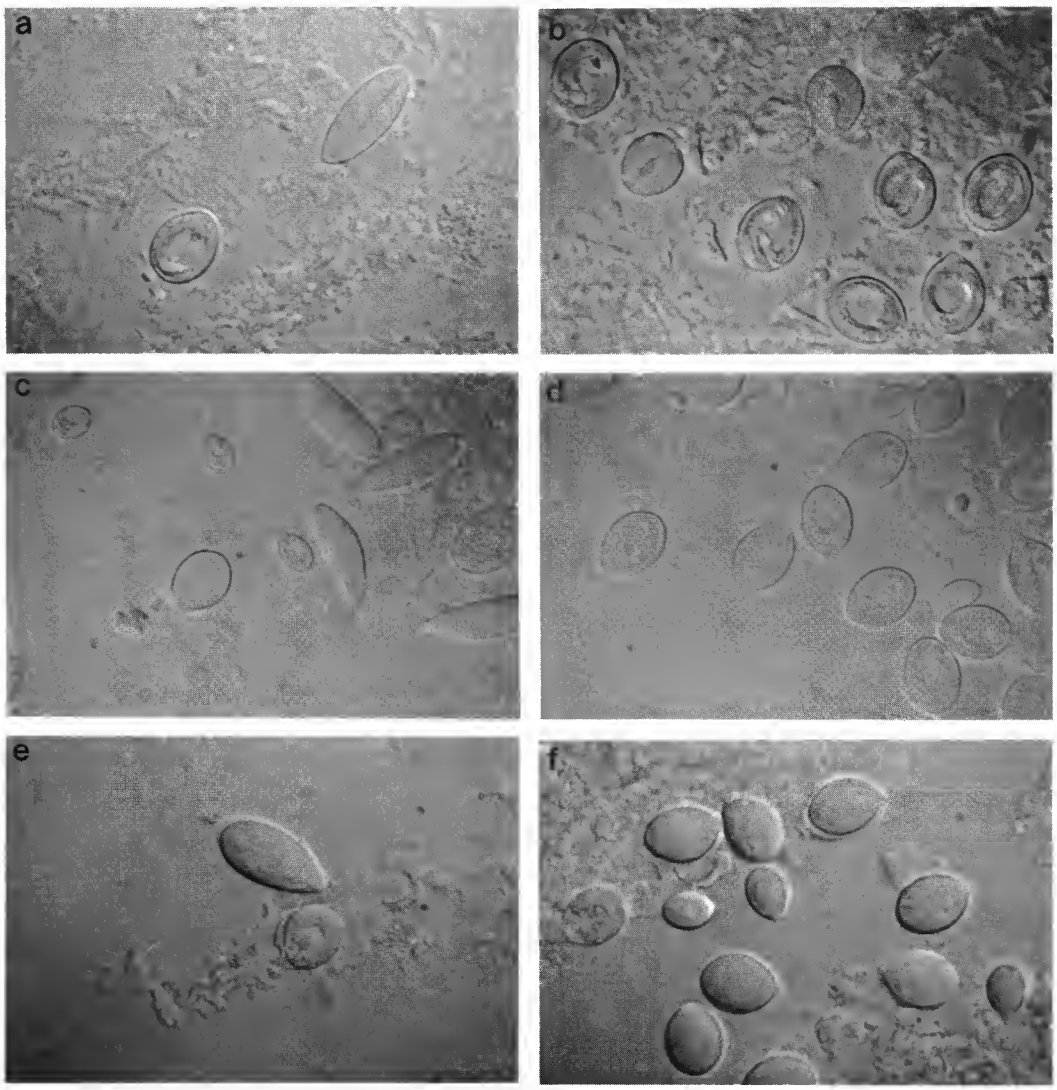


FIG. 2. — a, b, nematocysts of *Candelabrum serpentarii* nov. sp. (a, desmoneme and haploneme; b, six desmonenes, three stenoteles, one out of focus); c, d, nematocysts of *Candelabrum cocksii* (VIGURS, 1849) (c, four haplonemes, one large, five small desmonemes, and one stenotele; d, eleven large and two small desmonemes, two stenoteles, one partly); e, f, nematocysts of *Candelabrum phrygium* (Fabricius, 1780) (e, stenotele and haploneme; f, eight large and three small desmonemes, one stenotele). All nematocysts have been photographed with the aid of Nomarski interference contrast; × 750.

a, b, nématocystes de Candelabrum serpentarii *nov. sp. (a, desmonème et haplonème; b, six desmonèmes, trois sténotèles, un hors cadre); c, d, nématocystes de* Candelabrum cocksii *(VIGURS, 1849) (c, quatre haplonèmes, un grand et cinq petits desmonèmes, un sténotèle; d, onze grands et deux petits desmonèmes, deux sténostèles, un vu partiellement); e, f, nématocystes de* Candelabrum phrygium *(Fabricius, 1780) (e, sténostèle et haplonème; f, huit grands et trois petits desmonèmes, un sténostèle). Tous les nématocystes ont été photographiés à l'aide du microscope à contraste interférentiel Nomarski; × 750.*

been taken from ALLMAN's (1876) paper. It is not clear whether or not NAUMOV's (1960: 241-242, Figs 130, 131) notes on *Myriothela phrygia* refer to his own observations or those listed by (De) KOROTNEV. Certainly does NAUMOV's figure 130 refer to *Candelabrum cocksii*; it is taken from one of (De) KOROTNEV's plates and the claspers are distinctly visible. NAUMOV's figure 131, as he indicates, is taken from ALLMAN (1876) and refers to the actinula of *Candelabrum cocksii* [we have tacitly assumed that the major portion of detailed observations on *Myriothela phrygia* in NAUMOV's paper is based on solid observations (remarks on geographical distribution, bathymetrical record, life cycle, etc.)].

Candelabrum giganteum (Bonnevie, 1898)

Myriothela gigantea Bonnevie, 1898: 468, 490-491, Pl. 27 Figs 46-47; BONNEVIE, 1899: 9, 11, 37, 38, Pl. 4 Fig. 1; JÄDERHOLM, 1905: 7; BROCH, 1910: 194, 233, 236; MANTON, 1941: 143.

Candelabrum giganteum — STECHOW, 1922: 144, 1923: 45; HAND & GWILLIAM, 1951: 208.

LOCALITY. — Based on two more or less complete specimens and several fragments from deep water (2195 m) of the North Atlantic, 75°12'N-03°20'E.

REMARKS

Body elongated and thin, c. 300 mm long, basally thickest and slightly swollen, gradually tapering distally and terminating in fine filament. Below swollen or thickened basal portion a short, pointed foot with fine attaching filaments (no perisarc mentioned in original description). Blastostyles distributed over lower half of body; female blastostyles 10-20 mm long, with 1 or 2 big gonophores; male blastostyles shorter, 6-7 mm with many gonophores; both female and male gonophores have some terminal tentacles. Clavate tentacles on upper half of body, apparently also occurring in small numbers between blastostyles. Cnidome unknown. Curious filamentous appearance of distal part of body may be the result of inadequate fixation.

The species has not been rediscovered since the original description by BONNEVIE of specimens collected by the Norwegian North Atlantic Expedition 1876-1878.

Candelabrum harrisonii (Briggs, 1928)

Myriothela harrisonii Briggs, 1928: 312, Fig. 1, Pl. 33 Figs 1-2, Pl. 34 Fig. 5; BRIGGS, 1930: 5-14, Fig. 1, Pls 1-3, 1931: 270-278, Figs 1-3, 1939: 10.

Candelabrum harrisoni — HAND & GWILLIAM, 1951: 208.

LOCALITY. — Characterized as a "shallow water form, on underside of rocks below low-water mark at Bulli, 40 miles south of Sydney, N. S. W." (BRIGGS, 1928); number of individuals not stated.

REMARKS

Body cylindrical, elongated, divisible into foot, blastostyle bearing region and distal trunk. Foot set transversally towards length axis of body, with slender rooting processes, covered by translucent, chestnut-brown perisarc. Distal region of body cylindrical, slightly narrowing towards

blastostyle bearing region, with many capitate tentacles, diminishing in number towards blastostyle bearing zone. Blastostyles in single transverse row on swollen blastostyle region; that portion of body with fairly deep longitudinal furrows and fine transverse striae. Blastostyle with irregularly lobed base and a small number of gonophores (2-3 mature and 3-4 immature male gonophores; number in female unknown but less) with apical opening representing velar aperture. There is a single apical tentacle per blastostyle, often pushed aside by the developing gonophore. The size of the specimens is nowhere given in the description, nor can it be deduced from the figures. It probably had about the same size as *Candelabrum australe* with which it was simultaneously described.

Nematocysts described by BRIGGS (1930): desmonemes 10-12 × 8-9 µm; haplonemes 15-21 × 6-9 µm.

Candelabrum meridianum (Briggs, 1938)

Myriothela meridiana Briggs, 1938: 9-10, Pl. 15 Fig. 3; MILLARD, 1971: 399-401, Figs 1-2; STEPAN'YANTS, 1979: 26-27, Pl. 4 Fig. 4.

LOCALITIES. — "Six specimens 12-30 mm high attached to stones below low water, Macquarie Island" (BRIGGS, 1938). "Eight perfect or near-perfect individuals and about nine damaged specimens and fragments from below rock in the littoral region in Transvaal Cove, Marion Island", up to 27 mm long (MILLARD, 1971).

REMARKS

Original description by BRIGGS, 1939, supplemented by MILLARD, 1971. Species with tendency for subdivision of basal part of body, bi– or tripedal, fusion to single tubular distal region at c. one-third of height; body covered with small, capitate tentacles, continuing downward into blastostyle region at lower end of body. Base of body naked, occasionally ridged, "attached to substratum by a number of short adhesive tentacles each capped by a flat disc of brownish perisarc" (MILLARD, 1971). Blastostyles closely set, c. 2 mm long, occasionally branched once or twice, bearing 3-10 oval gonophores. Male gonophores sessile; female gonophores with short, thick stalk, larger than males, largest with 4-5 actinulae. Dioecious species. Cnidome described in detail by MILLARD (1971), composed of two size classes of oval desmonemes (11.3-14.9 × 8.7-11.3 and 6.2 × 5.2 µm), microbasic euryteles (14.9-16.5 × 5.7-6.1 µm), and other heteronemes (possibly stenoteles, 10.4-10.8 × 6.2-7.2 µm).

Candelabrum minutum (Bonnevie, 1898)

Myriothela minuta Bonnevie, 1898: 468, 489-490, Pl. 27 Fig. 44; BONNEVIE, 1890: 9, 35, 37, Pl. 3 Fig. 6a, b, Pl. 4 Fig. 4; JÄDERHOLM, 1905: 7; BROCH, 1910: 194, 233, 236; MANTON, 1941: 143.

Candelabrum minutum — STECHOW, 1922: 144, 1923: 45; HAND & GWILLIAM, 1951: 208.

LOCALITY. — Tromsö, northern Norway; no depth record.

REMARKS

Based on unknown number of specimens from Tromsö, where the species was found by M. SARS, apparently in the middle of the last century. Body small, cylindrical, thickest in middle (c. 2 mm), basally with pointed foot bearing attaching filaments; capitate tentacles only found in small number on extreme distal part of body and surrounding mouth. Blastostyles small, occurring on major part of body, bearing a single large (female) gonophore, the latter with a small, rudimentary tentacle. Cnidome unknown. The species has not been rediscovered since the original description.

Candelabrum mitra (Bonnevie, 1898)

Myriothela mitra Bonnevie, 1898: 468, 489, Pl. 27 Fig. 43; BONNEVIE, 1899: 9, 11, 33, 37, 38, 40, Pl. 3 Fig. 6c-e, Pl. 4 Fig. 3; JÄDERHOLM, 1905: 7; MANTON, 1941: 143.

Acandela mitra — STECHOW, 1920: 45, 1922: 144, 1923: 47.

Candelabrum mitrum — HAND & GWILLIAM, 1951: 208.

LOCALITY. — Based on a (male ?) specimen (or specimens) from deep water (2222 m) of the North Atlantic (63°22'N-05°29'W).

REMARKS

Body conical, basally widest, there 10 mm diameter, tapering distally, there 1-2 mm. Basal part of body with narrowly pointed, 10-20 mm long foot bearing rooting filaments; no perisarc described. Blastostyles on basal third to fourth of body, in many irregular whorls. Blastostyles conical, top with several capitate tentacles, curved; gonophores dispersed over blastostyle. There are no tentacles on rest of body.

The atentaculate condition of the body occasioned STECHOW (1920: 45) to institute a separate genus, *Acandela*, for its reception. This atentaculate condition may well result from damage sustained by the specimen studied by BONNEVIE. The number of specimens available to BONNEVIE is not unambiguously stated and may very well have been one single specimen, obtained in a haul from great depth. Moreover, in her 1898 paper BONNEVIE complains about the bad preservation of her specimen(s): "Das Ektoderm des Polypen hat eine eigenthümliche Struktur; und ich beklage, dass seine Konservirung nicht gut genug ist, um eine genauere Untersuchung zu gestatten, etc." (: 489). Loss of tentacles due to damage is also described by JÄDERHOLM (1905) for *Myriothela (= Candelabrum) austrogeorgiae*.

Candelabrum penola (Manton, 1940)

Myriothela penola Manton, 1940: 256-276, Figs 1-6, Pl. 1 Figs 10, 11, 14, Pl. 2 Figs 15-21, Pl. 3 Figs 22-26, 28, Pl. 4 Figs 29-34; BOUILLON, 1974: 143.

Candelabrum penola — BOUILLON, 1974: 143.

LOCALITY. — Based on two specimens, a mature female 850 mm long and an immature male of 55 mm body length, both found attached to the axis of a pennatulid and found floating alongside the research vessel *Penola* in a creek of the Argentine Islands, Graham Land, Antarctica.

REMARKS

MANTON describes the species as being dioecious. The following notes are based on the female specimen. Basal sixth of body, c. 100 mm long with a diameter of 12 mm, without tentacles and bearing numerous lobed blastostyles. Adhesive tentacles (rooting filaments) spring from basal part of body and some of proximal blastostyles and attach polyp to substrate; they are capped by a chitinoid disk; there is no perisarc. Female blastostyles 20-25 mm long, irregularly lobed or branched, with short, capitate tentacles (and on proximal blastostyles with some adhesive tentacles). Gonophores distributed over blastostyle, numbering up to 10; usually only one develops to maturity and is then quite large, 7.2 mm in diameter, considerably swollen by development of large actinula. Distal five-sixths of body, length c. 650 mm, diameter at oral end 7.5 mm, is covered by 0.5-2.5 mm long capitate tentacles; number estimated by MANTON at about 330,000.

The male specimen is quite young and will not be described here. The nematocysts are described by MANTON and consist of desmonemes of variable size (9-18 µm), haplonemes (13 × 9 µm) and heteronemes (10-18 × 7-13 µm).

Candelabrum phrygium (Fabricius, 1780)
(Figs 2e-f, 3E-F, Table 1)

Lucernaria phrygia Fabricius, 1780: 343; GMELIN, 1791: 3151.

Candelabrum [phrygium] — DE BLAINVILLE, 1830: 284, 1834: 318.

Candelabrum phrygium — L. AGASSIZ, 1862: 341; ALLMAN, 1864b: 358 (*Candelabrum Phrygia*); A. AGASSIZ, 1865: 186, 225, 226; STECHOW, 1922: 144; 1923: 45; KRAMP, 1932a: 5, 26, 1932b: 68, Tab. 1; 1943: 42; HAND & GWILLIAM, 1951: 208; CORNELIUS, 1977: 521 et seq.; STEPAN'YANTS, 1985: 85; ANTSULEVICH, 1987: 27; STEPAN'YANTS, 1989: 412 et seq.; CORNELIUS & RYLAND, 1990 116; ANTSULEVICH, 1991: 40; CAIRNS *et al.*, 1991: 16.

Myriothela phrygia — G. O. SARS, 1873: 86, 119; HINCKS, 1874: 136; G. O. SARS, 1874: 130, 140-142; LÜTKEN, 1875: 188; G. O. SARS, 1877: 26, note; M. SARS, 1877: 23, Pl. 2 Figs 29-36; STORM, 1879: 27; D'URBAN, 1880: 255, 257, 258; HINCKS, 1880a: 257; STORM, 1880: 122; WINTHER, 1880: 270; STORM, 1882: 8, 28, 30; ALLMAN, 1888: xxi, xliv; DRIESCH, 1890: 154; HARDY, 1891: 505-537, Figs 36-37; LEVINSEN, 1893: 150; VANHÖFFEN, 1897: 245; BONNEVIE, 1898: 491, 1899: 9, 11, 31, 33, 35, 37, 38, Pl. 4 Figs 5-6; BLACKBURN, 1899: 58-63, Pl. 8; WHITEAVES, 1901: 20; BROCH, 1903: Tab.; SWENANDER, 1904: 4-6; STEPHENS, 1905: 40; BILLARD, 1906: 5; JÄDERHOLM, 1908: 192, 233, 237; BROCH, 1910; 192, 233, 237; DERYUGIN, 1915: 304; BROCH, 1916: 19-21, Pl. 1 Figs 3, 8; HARTLAUB, 1916: 110, Figs 38-39; FRASER, 1918: 332, 341, 1921: 148, Fig. 18; SVARCHEVSKII, 1923: 99; CHADWICK, 1926: 51; MANTON, 1941: 143; FRASER, 1944: 88-89 [not Pl. 15 Fig. 63 = *Candelabrum cocksii* (Vigurs, 1849)]; BEREZINA, 1948: 50, Pl. 14 Fig. 1; REES, 1956: 116; NAUMOV, 1960: 241-243, Figs 130-131; CALDER, 1972: 222, Pl. 1 Fig. 5; CAMPBELL, 1974: 151, Fig. 9D; PETERSEN, 1990: 203.

Myriothela phrygia p.p. ALLMAN, 1872: 382 (excl. synonyms).

Corymorpha phrygia — MÖRCH, 1857: 24.

Myriothela arctica M. Sars, 1851: 126, 131, 134; ALDER, 1853: 35 (*Myristhela phrygia*); GOSSE, 1855: 20, Fig. 25; M. SARS, 1857: 192, 194; WRIGHT, 1858: 433, 1859: 108; M. SARS, 1860 (German translation): 342; HINCKS, 1861: 157; M. SARS, 1861: 693; ALLMAN, 1864a: 411, 1864c: 63; PARFITT, 1866: 5; VERRILL, 1879: 19; G. O. SARS, 1877: 26, note.

Myriothela arctica p.p. FORBES, 1854: 31 (excl. synonyms).

Candelabrum arcticum — ALLMAN, 1864b: 358.

Candelabrum arcticum p.p. L. AGASSIZ, 1862: 341 (excl. synonyms in part).

MATERIAL EXAMINED. — All specimens were obtained from the Lucky Strike hydrothermal vents area:

— two from the Lucky Strike cruise (site *Sintra*, marker 3, 37°17.50'N-32°16.47'W, 1622 m depth; dive 2606, June 1st, 1993; collected by Meg TIVEY); well preserved male specimens, both with developing male gonophores on blastostyles; one specimen attached to rock fragment (Fig. 3F), the other to a 20 mm long living specimen of mussel *Bathymodiolus* sp;

— seven from the Diva 2 cruise:

— two fixed and preserved in formalin (one female with large, mature eggs attached to blastostyles), obtained at dive PL 02, site *Sintra*, June 4, 1994; collected by Philippe CRASSOUS;

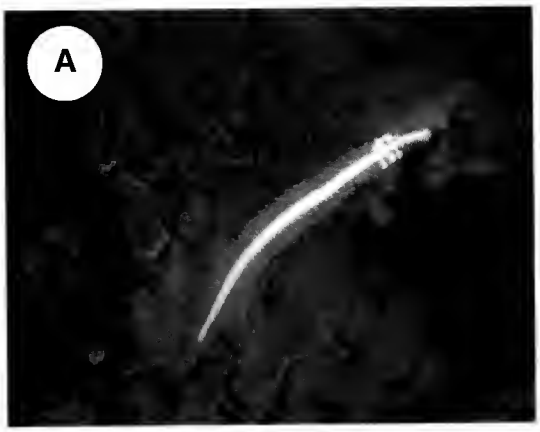
— two fixed in Bouin and tranferred to ethanol 70 %, from dive PL 09, site *Tour Eiffel* (37°17.31'N-32°16.51'W; 1690 m depth), June 11, 1994; collected by Luis SALDANHA. Also a basal part of a male specimen with many blastostyles with mature male gonophores, attached to a sulfide rock, and two parts of male specimen, the basal part with rock fragments and some developing gonophores, the second part a segment of the trunk with a complete, more or less digested shrimp[2] inside. The organic debris found in association with the three specimens of *Candelabrum phrygium* contains remnants of an amphipod, of a small shrimp, of a calanoid copepod, a complete healthy looking Ectinosomid (Copepoda Harpacticoida) and some unidentifiable animal remains;

— three (two females and a male: a 40 mm long female, eggs developing in gonophores; also a 65 mm long female with some large gonophores and rest of amphipod attached to tentacles; in addition, c. 50 mm long male, proximal part of trunk decomposed; blastostyle bearing region about as long as rest of trunk, with a great number of blastostyles bearing many developing and mature gonophores) preserved in formalin, from dive PL 10, site *Tour Eiffel*, June 12, 1994; collected by Marie-Claire FABRI.

2. This is probably a specimen of a newly described crustacean *Chorocaris fortunata* (MARTIN & CHRISTIANSEN, 1995, L. B. Holthuis, pers. comm.); TL c. 10 mm, diameter 2-3 mm.

FIG. 3. — A: *Candelabrum serpentarii* nov. sp. (length c. 10 cm), Snake Pit area, next to *Élan* site, 3515 m, on sulfide rock, surrounded by polychaete tubes; B: *Candelabrum serpentarii* nov. sp. (length c. 8 cm), Snake Pit area, next to *Les Ruches* site, 3505 m, on sulfide rock, surrounded with tubes of polychaeta Chaetopteridae and Zoantharia (Cnidaria); C: *Candelabrum serpentarii* nov. sp. (paratype, length c. 7.5 cm), Snake Pit area, next to *Les Ruches* site, 3523 m, on pillow lava; D: The same specimen, freshly collected, natural colours (however, one can notice the difference of colour with *in situ* organism of photo A); the black spots are sulfidic metal particles precipitated on the animal in the slurp gun box; E: *Candelabrum phrygium* (FABRICIUS, 1780), length 7-9 cm, Lucky Strike area, *La Pagode* site, 1626 m, on flange mineral formation covered with white silica; one mussel (*Bathymodiolus* sp.) is visible; F: *Candelabrum phrygium* (Fabricius, 1780), Lucky Strike area, *Sintra* site, 1622 m, on flange block.

A: Candelabrum serpentarii *nov. sp. (L = env. 10 cm), zone du Snake Pit, près du site* L'Élan, *3515 m, sur un bloc de sulfure, entouré de tubes de polychètes; B:* Candelabrum serpentarii *nov. sp. (L = env. 8 cm), zone du Snake Pit, près du site des* Ruches, *3 505 m, sur un bloc de sulfure, entouré de tubes de polychètes Chaetopteridae et de zoanthaires (Cnidaires); C:* Candelabrum serpentarii *nov. sp. (paratype, L = env. 7,5 cm), zone du Snake Pit, près du site des* Ruches, *3 525 m, sur des laves en coussin; D: le même spécimen, fraîchement récolté, couleurs naturelles (on notera toutefois la différence de couleur avec l'organisme* in situ *de la photo A); les taches noires sont des particules de sulfures métalliques précipités sur l'organisme dans le collecteur du système d'aspiration; E:* Candelabrum phrygium *(FABRICIUS, 1780), L = 7-9 cm, zone de Lucky Strike, site de* La Pagode, *1 626 m, sur formation minérale "flange", couverte de silice blanche; une moule (*Bathymodiolus *sp.) est visible; F:* Candelabrum phrygium *(Fabricius, 1780), zone de Lucky Strike, site* Sintra, *1 622 m, sur un bloc de "flange".*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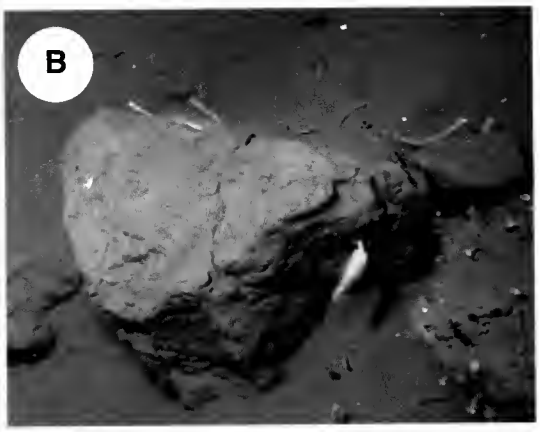
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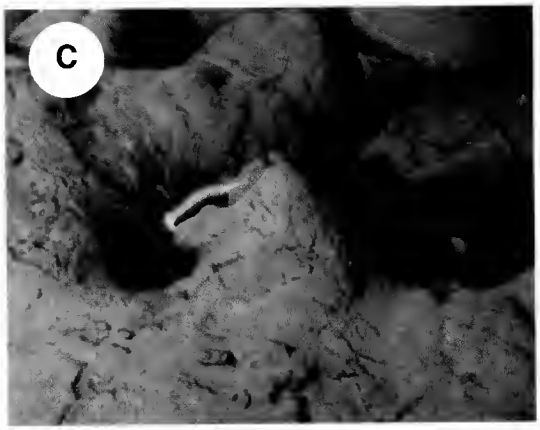
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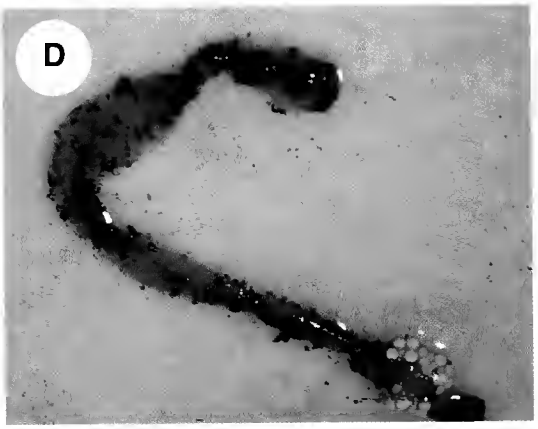
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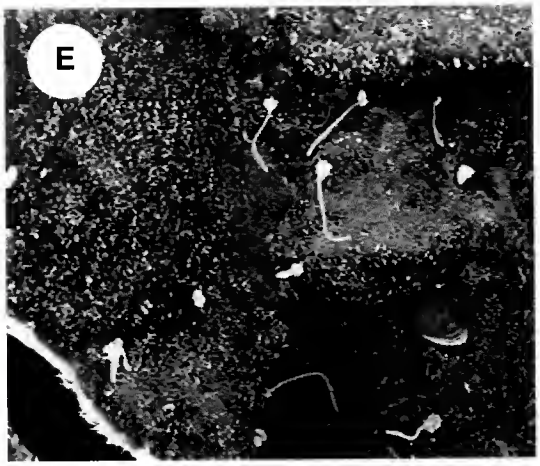
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F

DIAGNOSIS

Body composed of foot, blastostyle bearing region and trunk. Foot: a lobed, flattened part of body, attaching animal to rock or substrate (bivalve molluscs), without chitinous adhesive portion. Blastostyle bearing region forming lower third to fourth of body, with a large number (10 to 15) of big, tubular blastostyles, bearing male gonophores in various stages of development and dispersed, capitate tentacles; apex of each blastostyle with circle of 4 or 5 tentacles. Remainder of body forming elongated, tubular trunk, completely covered by capitate tentacles. Mouth distinct, at end of trunk.

DESCRIPTION

All specimens available are attached to rock fragments, one male is attached to the exterior of a living bivalve. In all specimens the foot attaches the body to the substrate; there are no chitinous adhesive disks or chitinous portions of the foot. In the specimen on the mollusc, the foot is more distinctly lobed than in the others. Directly above the foot is the blastostyle bearing part of the body, 12-15 mm high and bearing a considerable number (10 to ca. 50 in the male, usually less in the female) of tube-shaped blastostyles, the body cavity continuing into the blastostyles. Male and female blastostyles are found on separate polyps; the species consequently is dioecious. Each male blastostyle is 8-10 mm long and carries many developing male gonophores, with dispersed, capitate tentacles in between. The apex of each blastostyle carries a circle of 4 or 5 capitate tentacles. Male gonophores 0.40-0.80 mm in diameter, attached by means of thin tissue strand and easily detached in the preserved specimens, apparently filled with developing spermatocytes. The female blastostyles are shorter and thinner than the males and have less gonophores. In the specimens inspected each blastostyle has gonophores in various stages of development, the youngest in the basal part, the mature gonophores at the top; there are only few tentacles. The smallest gonophores measured are 0.40 mm, the largest, apparently mature gonophores are 1.40 mm. The gonophores that have been supposed to be mature contain a single, large egg; it is attached to the blastostyle by means of a thin strand of tissue, being the continuation of a thin layer of tissue covering the egg. Trunk vermiform, diameter c. 2.5 mm, in the preserved specimens 25-30 mm long, completely covered by short, capitate tentacles. Each tentacle has a 0.35-0.50 mm long pedicel and a capitulum of 0.17-0.25 mm diameter; nematocysts dispersed over capitulum.

Nematocysts studied in squash preparations of capitulum of trunk tentacles, composed of two size classes of desmonemes, haplonemes and stenoteles.

Haplonemes slightly longer than those of *C. serpentarii*, but of the same general shape: elongated ovoid and slightly narrowed apically, as a result more or less pyriform, 19.7-20.5 × 8.2-9.9 µm, found more frequently than in capitulum of *C. serpentarii*. Internal structure fairly obscure, but a longitudinally descending shaft and oblique coils of the thread could be observed.

Desmonemes of two size classes occur in profusion, the larger being almost identical with those of *C. serpentarii*, broadly ovoid, slightly asymmetrical apically and there with a slight elevation just outside middle of top, 12.5-13.0 × 9.0-9.8 µm. The smaller type is slightly more elongated, 8.2-9.0 × 6.4-6.6 µm. Both types with a thick thread in irregular coils; in desmonemes in perfect lateral view part of thread parallel to internal wall of basal portion. Both types were found to occur in almost equal numbers.

Stenoteles scarce and apparently badly preserved, as internal structure was quite obscure; they could best be recognized by the flattened top (when in good position), 10.6-11.5 × 8.2. × 9.8 µm. Details of shaft and thread could not be discerned. It was difficult to estimate the occurrence of stenoteles because of bad preservation: they could only with certainty be distinguished from desmonemes when in good position to see apical flattening.

REMARKS

The various locality records are not specified here. The species is circumarctic, occurring in both Atlantic (BONNEVIE, 1898-99: Norwegian North Atlantic Expedition, Stn 303, 75°12'N-03°02'E, 2195 m) and Pacific (NAUMOV, 1960) parts of the Arctic seas. In the Atlantic at least it also penetrates boreal waters, though there usually at greater depths. It is now also known to occur in deep water of the NE Atlantic.

The Lucky Strike specimens were generally found at the base of the active edifices, attached to organic support (shell of living bivalve) or, more frequently, to mineral formations called "flanges" and composed of a mixture of pyrite, marcasite and baritine, with sometimes some white silica at the surface. The specimens are frequently observed at the site *Sintra*, but they occur also at the site *Tour Eiffel*. At the *Pagode* site 7 or 8 individuals were observed together on 0,5 m^2 (Fig. 3E). At that locality, a few animals (mussels, crabs and shrimps) are present, but generally the surrounding faunal community is largely composed of bivalved Mytilidae (*Bathymodiolus*) (VAN DOVER *et al.*, submitted), shrimps (Alvinocarididae), crabs (Bythograeidae) and several smaller Crustacea (Copepoda Siphonostomatoida, Amphipoda) living in a mixture of sea water and hydrothermal fluid (loaded with sulfurous compounds), mean temperature ca. 11° C. Other animals observed at the Lucky Strike hydrothermal vents area include sponges (*Cladorhiza* sp.) and hydroids (*Eudendrium* sp.), both found on the top of the inactive edifices. In many cases these animals carry white, filamentous bacteria.

Candelabrum serpentarii nov. sp.

(Figs 2a-b, 3A, B, C, D, 4, Table 1)

MATERIAL EXAMINED. — One complete specimen, total body length 75 mm, and a 40 mm long upper part of body of second specimen, both from the Hydrosnake cruise at the Snake Pit hydrothermal area (site *Les Ruches*, 23°23'N-47°57'W, 3489 m depth, dive HS 10, June 28, 1988; collected by M. S.). Specimen with large female and smaller male gonophores and presently slightly deteriorated because of frequent inspections; chitinous covering of foot lost; remains in National Museum of Natural History, Leiden (paratype, RMNH Coll. No 27111).

Well preserved specimen in three parts, total body length c. 80 mm, composed of basal body region with gonophores (in two parts) and trunk, from the MAR 93 cruise next to the site *Élan* in the Snake Pit area, about 30 m to the west of the site *Les Ruches* (dive 2619; 3525 m depth, June 20, 1993; collector: Jean-Paul Truchot). This specimen was fixed in Bouin and later on transferred to ethanol 70%, now preserved in Muséum national d'Histoire naturelle, Paris (holotype, MNHN Hy No 1133).

ETYMOLOGY. — *serpentarii*, from the Latin *serpentarium*, snake pit.

DIAGNOSIS

Large *Candelabrum;* total body length 60-80 mm, attached to solid substrate by means of laterally flattened, basal foot covered by thick, curved, brownish-black perisarcal sheath. Rest

of body composed of proximal region bearing large blastostyles each bearing a number of male and female gonophores in various stages of development, and an elongated trunk completely covered with short, capitate tentacles. Capitulum of each tentacle with distal layer of nematocyst bearing ectoderm. Cnidome (of capitate tentacles) composed of desmonemes (predominant), large haplonemes and two size classes of stenoteles, of which the smaller class has only occasionally been observed.

DESCRIPTION

Since none of the specimens is fully intact, parts of the following description are the result of reconstruction.

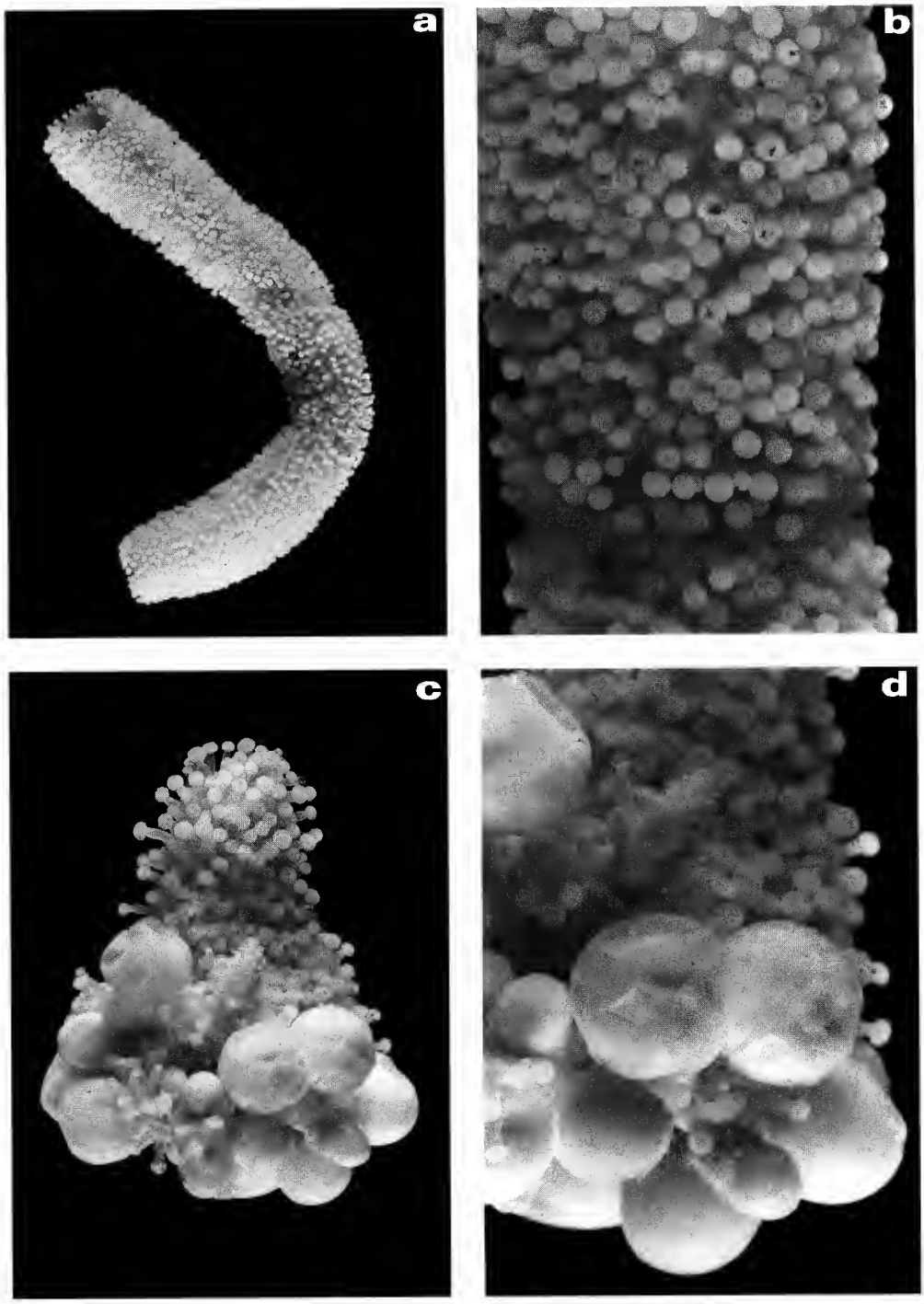
The c. 60 mm long body can be divided into a foot, a blastostyle bearing region and the apical trunk. The foot has only been observed in the paratype (Fig. 2), where it is a laterally flattened, rounded portion of the body, attaching the polyp to the hard substrate (pillow lava) by a considerable portion of its surface. The foot was covered by a thick, brownish-black, c. 1 mm thick perisarcal shield, at first firmly attached to the foot, but later on spontaneously loosening itself. No perisarcal threads with or without apical button, attaching the foot to the rock have been observed.

The blastostyle bearing zone of the body has about the same diameter as the trunk (c. 7 mm), the body cavity continues in that zone and in the blastostyles, that represent lateral, tentacle bearing elevations of the body wall. Blastostyles 3-5 mm long, with c. 10 male and 3-5 apparently fully mature female gonophores. The tentacles observed on the body between the blastostyles as well as those on the blastostyles (between the gonophores and at the apex) are indistinguishable from those on the trunk. Male gonophores c. 1-1.5 mm in diameter, apparently filled with developing spermatocytes. The female gonophores are large, 4-5 mm in diameter, attached to the blastostyle by means of a short, stubby neck and surrounded by an opaque layer of ectodermal cells; no nematocysts having been observed. The large egg can be dislodged by carefully cutting the ectodermal covering; the egg in the well preserved specimen from the Snake Pit appeared to be entirely filled with yolk with many fat goblets and was surrounded by a hyaline membrane. No structure could externally be observed and it is presumed that the eggs, at least in this specimen, are still unfertilized. No traces of claspers or aberrant tentacles could be found in the blastostyle bearing zone.

The trunk is a tube-like expansion of the body externally fully covered by capitate tentacles. The lumen of the gastral cavity is considerable; the mouth at the end of the trunk is closed. The tentacles consist of a short, 0.6-0.8 mm long stalk and a globular capitulum of 0.4-0.6 mm diameter; the apex of the capitulum is covered by a semiglobular layer of ectodermal cells with

FIG. 4 — *Candelabrum serpentarii* nov. sp., holotype, from Snake Pit area; a, distal part of body, completely covered with small, capitate tentacles; b, close up of the capitate tentacles; c, proximal part of body with capitate tentacles on distal zone and blastostyles, with male and female gonophores, as well as capitate tentacles, on the basal zone; d, close up of one of the gonophores.

Candelabrum serpentarii *nov. sp., holotype, provenant du Snake Pit; a, partie distale du corps, complètement recouvert de petits tentacules capités; b, détail des tentacules capités; c, partie proximale du corps avec des tentacules capités au niveau de la zone distale et des blastostyles, avec des gonophores mâles et femelles sur la partie basale; d, détail des gonophores.*


a
b
c
d

many nematocysts. The tentacular stalks, as can be seen from the photographs of living specimens, are hightly contracted in the preserved specimens, the capitulum standing off a distance of several mm from the body surface.

The nematocysts have been studied in squash preparations of the capitulum of tentacles of the trunk. There appear to be three types of nematocysts: haplonemes, stenoteles and desmonemes.

Haplonemes elongated ovoid, slightly narrowed distally and as a result also a bit pyriform and slightly asymmetrical, 16.5-18 × 7.8-8.2 µm, rather uniform of size and shape. They have not been found in exploded condition, consequently the characters of the thread could not be studied. In unexploded condition the thread is seen to descent from the apex down to the bottom in a straight line; the rest of the thread is coiled in obliquely transverse coils.

Stenoteles almost globular, in perfect position observed to be broadly ovoid, perfectly symmetrical, with indistinctly flattened top. Shaft and barbs forming a central column in the unexploded capsule and about three-fourth the height of the capsule; thread in indistinct transverse coils in the basal third of the capsule. Size 9.8-11.5 × 9.5-10.5 µm. A second type of stenotele has occasionally been observed, but only in exploded condition, the capsule measuring 5.4 × 7.4 µm. Details of barbs and thread could not be observed.

Desmonemes broadly ovoid, but for the apical protrusion almost perfectly symmetrical, 13-14.5 × 9.8-10.5 µm. Apical protrusion low, slightly besides middle of apex; thread thick, forming a small number of loose coils following the internal desmonemal wall.

In the tentacular capitulum the desmonemes predominate; haplonemes and (large) stenoteles forming c. 5 % of the capsular number. The smaller stenoteles have only occasionally been observed.

REMARKS

In the Snake Pit field the occurrence of this species is restricted to an area of several meters from an active structure and it is not observed outside a radius of some twenty or thirty meters. The species may thus be considered to indicate the proximity of hydrothermal activity, though one individual has been observed at inactive vents. Depending upon the proximity of the active sites the specimens are attached to pillow lava (Fig. 3C) or sulfide rocks (Fig. 3A-B). They are quite irregularly distributed, occasionally 2 or 3 individuals are found within one meter distance. At this level there are probably no thermal anomalies, the temperature at those abyssal depths being generally 2.4° C. Surrounding fauna is scarse (SEGONZAC, 1992), composed of some fishes (Pisces Synaphobranchidae), galatheides (Crustacea Galatheidae), and occasionally one or two isolated shrimps (*Rimicaris exoculata*), Williams & Rona, 1986 (Crustacea Alvinocarididae).

Candelabrum tentaculatum Millard, 1966

Myriothela tentaculata Millard, 1966: 437-440, Fig. 2; BOUILLON, 1974: 143; MILLARD, 1975: 46-48, Figs 17C, 18B-E; 1978: 195 et seq., 1979: 134.

LOCALITY. — Based on five specimens from off Slangkop on west coast of Cape Peninsula, 34°09.3'S-18° 17.5'E, 24 March 1959, 43 m depth.

REMARKS

Body up to 31 mm long, attached to encrusting Bryozoa by means of nine short, adhesive processes capped by chitinoid discs springing from irregularly shaped basal portion. Blastostyles in single whorl of 17, reaching 20 mm length, with c. 25 rather poorly developed capitate tentacles on distal region and scattered amongst 4-6 gonophores on proximal 5 mm. Only male gonophores known, species apparently dioecious. Rest of body densely covered with capitate tentacles. Cnidome adequately described by MILLARD (1975) and composed of heteronemes (up to 45 µm long!), two size classes of desmonemes, stenoteles and atrichous isorhizas.

Candelabrum verrucosum (Bonnevie, 1898)

Myriothela verrucosa Bonnevie, 1898: 468, 490, Pl. 27 Fig. 45; BONNEVIE, 1899: 9, 37, Pl. 4 Fig. 2.

Candelabrum verrucosum — STECHOW, 1922: 144, 1923: 45; HAND & GWILLIAM, 1951: 208.

LOCALITY. — No locality mentioned in original description (BONNEVIE, 1898), but in BONNEVIE's 1899 paper the species is mentioned in a table and Hammerfest (Norway) is given as the locality; there is no (definite) depth record.

REMARKS

Small species, total body length c. 40 mm, diameter 1-2 mm, thickest just under mouth. Attached by means of attaching filaments springing from basal part of body. Lower fifth of body bearing blastostyles, rest of body covered with capitate tentacles. Blastostyles short, with one or two gonophores and with tentacles distally. Gonophores with dispersed clusters of nematocysts over their surface. The species may be based on a single specimen (number of specimens or variability not stated); it should be recognizable by the clusters of nematocysts on the gonophores, though according to Bonnevie these are difficult to perceive!

Candelabrum sp. 1

Myriothela (?) HICKSON & GRAVELY, 1907: 18-19, Pl. 3 Fig. 18.

LOCALITY. — Based on single specimen from Winter Quarters of Discovery expedition, Hut Point, McMurdo Sound, Ross Sea, 13 October1902 (Hickson & Gravely, 1907).

REMARKS

Composed of c. 8 mm long hydrocaulus, 2 mm in diameter, basally with numerous filaments attaching specimen to debris of sponge spicules. Body of hydranth c. 6 mm long, spindle shaped, thickening from hydrocaulus and tapering apically to form conical hypostome. Distal half of hydranth covered with short, thick capitate tentacles. No blastostyles or gonophores developed on proximal part of body. Might turn out to be a juvenile specimen of one of the antarctic species.

Candelabrum sp. 2

Candelabrum spec. HAND & GWILLIAM, 1951: 207, 208.
Candelabra sp. AUSTIN, 1985: 46 (sic).

LOCALITY. — Three specimens were found in a pholad hole on the undersurface of a rock at mean lower water at Pigeon Point, San Mateo County, California, USA, 6 May 1950.

REMARKS

Based on three not fully mature specimens. The description by HAND & GWILLIAM (1951) is repeated here verbatim: "Hydranth: Not branched, solitary, naked, and arising from a creeping hydrorhiza or possibly a disc. Hydrorhizae invested with perisarc. Exclusive of hydrorhizae, polyp divisible into two zones; a distal tentacle-bearing zone and a proximal tentacle-free blastostylar zone. The tentacle-bearing zone composes five-sixths or more of the polyp length and bears approximately 500 tentacles in the adult; cylindrical, approximately the same diameter throughout. Tentacles densely packed, short, capitate and not arranged in any discernible pattern. Mouth terminal. Blastostylar zone swollen, of a slightly greater diameter than the tentacle bearing zone. Sometimes separated from tentacle-bearing zone by a constriction; at the proximal end tapering sharply to hydrorhiza. Structures referred to by ALLMAN (1875) as claspers not present on specimens examined. Blastostyles giving rise to more than one gonophore. Largest specimen (preserved) 2.5 cm long by 0.15 cm in diameter (including the tentacle)".

Compared by HAND & GWILLIAM with *Candelabrum harrisoni* Briggs, which it resembles closely.

Candelabrum sp. 3

Dr Chad HEWITT and Dr GODDARD (University of Tennessee, USA) recently informed us that they will describe a species of *Candelabrum* from intertidal waters of the Pacific coast of Oregon.

ECOLOGICAL REMARKS

1 — *Trophic behaviour.*

As stated above, a fairly large (c. 10 mm TL), partly decomposed shrimp (*Chorocaris fortunata* Martin & Christiansen, 1995) was found in the enteron of a specimen of *Candelabrum phrygium*, demonstrating their ability to capture large preys, as also indicated by their considerable armament. This, and the presence of other small Crustacea (Amphipoda and Copepoda Siphonostomatoida) in their immediate vicinity, makes it likely that they can be considered to prey upon the Lucky Strike faunal community.

Candelabrum serpentarii, on the contrary, does not actually live in a hydrothermal habitat. It was found outside but close to the active sites, in an area deprived of visible fauna and

consequently less rich in prey. The absence (noticed during the submersible explorations) of *C. serpentarii* outside an area of 20 or 30 m radius of the active sites leads to the consideration that the species, directly or indirectly, benefits from the active sites communities. It has been observed that an important bacterial production (both free and associated with invertebrates) gives rise to a community largely dominated by the shrimp *Rimicaris exoculata* (SEGONZAC *et al.*, 1993). Though the type of food consumed by *C. serpentarii* so far has not been observed directly, it seems reasonable to suggest that, as in *C. phrygium*, it consists mainly of shrimps and other small Crustacea. The metabolism, in this animal, might be adapted to the occasional capture of (large) preys, as is the case in many abyssal predators.

It should be remembered that in *Candelabrum* the number of tentacles is considerable, the nematocysts being concentrated in the tentacular capitulum. As indicated above the considerable amount of nematocysts allows the capture of large preys, for which action the haplonemes, stenosteles and heteronemes, if present, are responsible. The numerous desmonemes may serve for the attachment of preys, that can either be transported to the mouth or swallowed after curvature of the trunk towards the place of attachment. Many athecate hydroids have an extensible mouth capable of devouring a prey of considerable size. The *Candelabrum* species probably are no exception in this respect.

2 — *Biogeography.*

Most *Candelabrum* species live in intertidal waters. Geographical distribution in the members of this genus is usually restricted by the absence of a planktonic stage and by the necessity to be attached to hard substrates. The circumarctic distribution of *C. phrygium,* which has a non-planktonic actinula larva, is not in agreement with the ecological status observed on the Lucky Strike site. Indeed, its distribution there is restricted to areas of active venting (living in a mixture of sea water and hydrothermal fluid loaded with sulfurous compounds, mean temperature: 11° C). Moreover, direct observations and video analysis indicate the absence of individuals outside the sites. It is thus difficult to understand why this species, is strongly linked to such peculiar and very confined physical and chemical conditions.

The status of *C. serpentarii* is likewise difficult to explain, but it is different. As stated above, this species has affinities with *C. cocksii*, a species only known from the NE Atlantic intertidal zone. Both species have low dispersal abilities (the fertilized eggs develop into the actinulae before they separate from blastostyles); they were never observed or collected on the abyssal plains.

Considering those facts, and bearing in mind the difficulties in understanding the colonization processes without fossil records, the isolation of the various *Candelabrum* populations could be explained in terms of plate tectonics viz. the movement of oceanic plates. For example, it could be hypothesized that *Candelabrum serpentarii* results from allopatric speciation (with the preservation of several morphologic features and the mode of reproduction) from an ancient intertidal stock of *C. cocksii* (or, more likely, a common ancestral form) that became isolated as a result of the successive events that led to the rifting and further spreading of the Atlantic Ocean floor. One of the populations may progressively have adapted to the deep hydrothermal environment where the hard substrate and the trophic conditions represented favourable living conditions.

In order to answer questions concerning the present distribution of these species of *Candelabrum*, several kinds of studies should be carried out:

1) a profound study leading towards a better understanding about their life-cycle;

2) a study of the deep water circulation pattern in this part of Atlantic Ocean;

3) the exploration of other ridge segments to gain additional records of species of *Candelabrum*.

Technical aid

All *C. cocksii*, *C. phrygium* and *C. serpentarii* nematocysts (Fig. 2) have been photographed by Dr J. C. DEN HARTOG (Nationaal Natuurhistorisch Museum, Leiden). Fig. 3D-F and Fig. 4 were made from photographs taken by Patrick BRIAND (IFREMER). The map shown in Fig. 1 was realized by Violaine MARTIN (IFREMER). The pictures Fig. 3A, B, C and E, partly resulting from videotape enlargements, were placed at our disposal by Gérard VINCENT and Valérie BATY (Picture library, IFREMER).

Acknowledgements

The authors wish to express their gratitude to the chief scientists: A.-M. ALAYSE, D. DESBRUYÈRES, J. DUBOIS, A. FIALA, C. LANGMUIR, C. MÉVEL and C. VAN DOVER, as well as the crews of both the research vessels and the submersibles, that participated in the cruises, Dr A. CASTRIC-FEY (Concarneau) who kindly placed specimens of *C. cocksii* at our disposal, Dr J. C. DEN HARTOG (Leiden), Patrick BRIAND, Violaine MARTIN, Gérard VINCENT and Valérie BATY (IFREMER) for their technical aid, and the authorities of the National Museum of Natural History where research on the specimens was partly carried out.

The specimens of *C. serpentarii* and *C. phrygium* originate from cruises Hydrosnake, Lucky Strike, MAR 93, Gravinaut and Diva 2 organized by INSU, IFREMER and WHOI institutions within the framework of the FARA program (French American Ridge Atlantic).

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Sur les *Oswaldocruzia* (Nematoda, Trichostrongylina, Molineoidea), parasites d'amphibiens et de lézards de Cuba et de Porto Rico

par Badreddine BEN SLIMANE et Marie-Claude DURETTE-DESSET

Résumé. — L'examen d'*Oswaldocruzia* de Cuba et de Porto Rico montre l'existence de quatre espèces différentes. *O. lenteixeirai* Vigueras, 1938, dépourvue d'ailes cervicales, possède des côtes bursales 8 chevauchées par les côtes 6 dans leurs deux tiers proximaux et des côtes bursales 5-6 jointives ; mâle avec 32-38 crêtes cuticulaires au milieu du corps ; vestibule pourvu de formations distales. *O. moraveci* n. sp. (= *O. lenteixeirai sensu* BARUS et MORAVEC, 1967, *nec* VIGUERAS, 1938) se différencie de la précédente par des côtes bursales 8 chevauchées par les côtes 6 dans leur partie médiane et des côtes bursales 5-6 divergentes à leur extrémité ; vestibule dépourvu de formations distales. *O. anolisi* Barus et Coy Otero, 1968, pourvue de grandes ailes cervicales, possède des côtes bursales 8 chevauchées par les côtes 6 dans leur partie médiane et des côtes bursales 5-6 jointives ; mâle avec 50 crêtes cuticulaires au milieu du corps ; vestibule dépourvu de formations distales. *O. barusi* n. sp., pourvue d'ailes cervicales peu développées, possède des côtes bursales 8 chevauchées par les côtes 6 dans leur partie médiane et des côtes bursales 5-6 jointives ; mâle avec 38 crêtes cuticulaires au milieu du corps ; vestibule dépourvu de formations distales.

Mots-clés. — *Oswaldocruzia*, Nématodes, Trichostrongylina, Amphibiens, Lézards, Antilles.

On *Oswaldocruzia* spp (Nematoda: Trichostrongylina-Molineoidea), parasites of amphibians and lizards from Cuba and Puerto Rico

Abstract. — Four different species of *Oswaldocruzia* have been identified from Cuba and Puerto Rico. *O. lenteixeirai* Vigueras, 1938, without cervical alae, with rays 8 joined to rays 6 along the proximal two thirds and with rays 5 and 6 close together; male with 32-38 cuticular crests in the mid body; vestibule with distal formations. *O. moraveci* n. sp. (= *O. lenteixeirai sensu* BARUS et MORAVEC, 1967, *nec* VIGUERAS, 1938) differentiated from the former by rays 8 overlapped by rays 6 along their median part and by the divergency of the extremities of rays 5 and 6; vestibule without distal formations. *O. anolisi* Barus et Coy Otero, 1968, with developed cervical alae; with rays 8 overlapped by rays 6 along their median part and with rays 5 and 6 close together; male with 50 cuticular crests in the mid body; vestibule without distal formations. *O. barusi* n. sp., with poorly developed cervical alae; with rays 8 overlapped by rays 6 along their median part and with 5 and 6 rays close together; male with 38 cuticular crests in the mid body; vestibule without distal formations.

Keywords. — *Oswaldocruzia*, Nematoda, Trichostrongylina, Amphibians, Lizards, West Indies.

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INTRODUCTION

Le genre *Oswaldocruzia* (44 espèces connues) est un parasite cosmopolite d'Amphibiens et de Reptiles. Il a été créé par TRAVASSOS (1917) avec pour espèce type *O. subauricularis*. Deux espèces ont été décrites et identifiées de diverses îles des Antilles : *O. lenteixeirai* Vigueras, 1938, à Cuba et Porto Rico et *O. anolisi* Barus et Coy Otero, 1968, à Cuba. Cependant, en

1968, BARUS & COY OTERO ont mis *O. anolisi* en synonymie d' *O. lenteixeirai* en se basant sur le travail de MORAVEC & VOJTKOVA (1975) car ces auteurs estimaient que la présence ou l'absence d'ailes cervicales n'était pas un bon caractère spécifique. Depuis cette époque, plusieurs publications (DURETTE-DESSET, NASHER & BEN SLIMANE, 1992, BEN SLIMANE, DURETTE-DESSET & CHABAUD, 1993) se fondant sur des coupes transversales du corps montrent que, en plus de leurs dimensions, les ailes cervicales peuvent être constituées par un nombre spécifique de crêtes cuticulaires et avoir une forme spécifique.

Il nous a donc paru utile, en utilisant ce caractère, de reprendre les différents travaux concernant ces deux espèces.

Grâce à l'obligeance du Pr MORAVEC et du Dr LICHTENFELS, que nous remercions très vivement, nous avons obtenu les différents spécimens qui sont étudiés ci-dessous.

MATÉRIEL ET MÉTHODES

Les spécimens, conservés dans l'alcool à 70°, sont étudiés dans de l'eau ou du lacto-phénol plus ou moins dilué. Lorsque le matériel est suffisamment abondant, les coupes transversales du corps et la dissection des spicules sont réalisées selon les techniques de DURETTE-DESSET (1985).

La nomenclature utilisée pour la bourse caudale est celle de DURETTE-DESSET & CHABAUD (1981), pour l'étude du trajet des côtes 8 par rapport aux côtes 6, celle de DURETTE-DESSET *et al.* (1992). La nomenclature du synlophe dans la région œsophagienne et des spicules sont celles de BEN SLIMANE *et al.* (1993).

REDESCRIPTION DES ESPÈCES

Oswaldocruzia lenteixeirai Vigueras, 1938

MATÉRIEL DE REDESCRIPTION. — 1 mâle en deux morceaux et 1 femelle United States National Museum, Helminthological Collections, n° 73235.

Hôte : *Eleutherodactylus portoricensis* Thomas, 1966 (Leptodactylidae).

Localisation : intestin grêle.

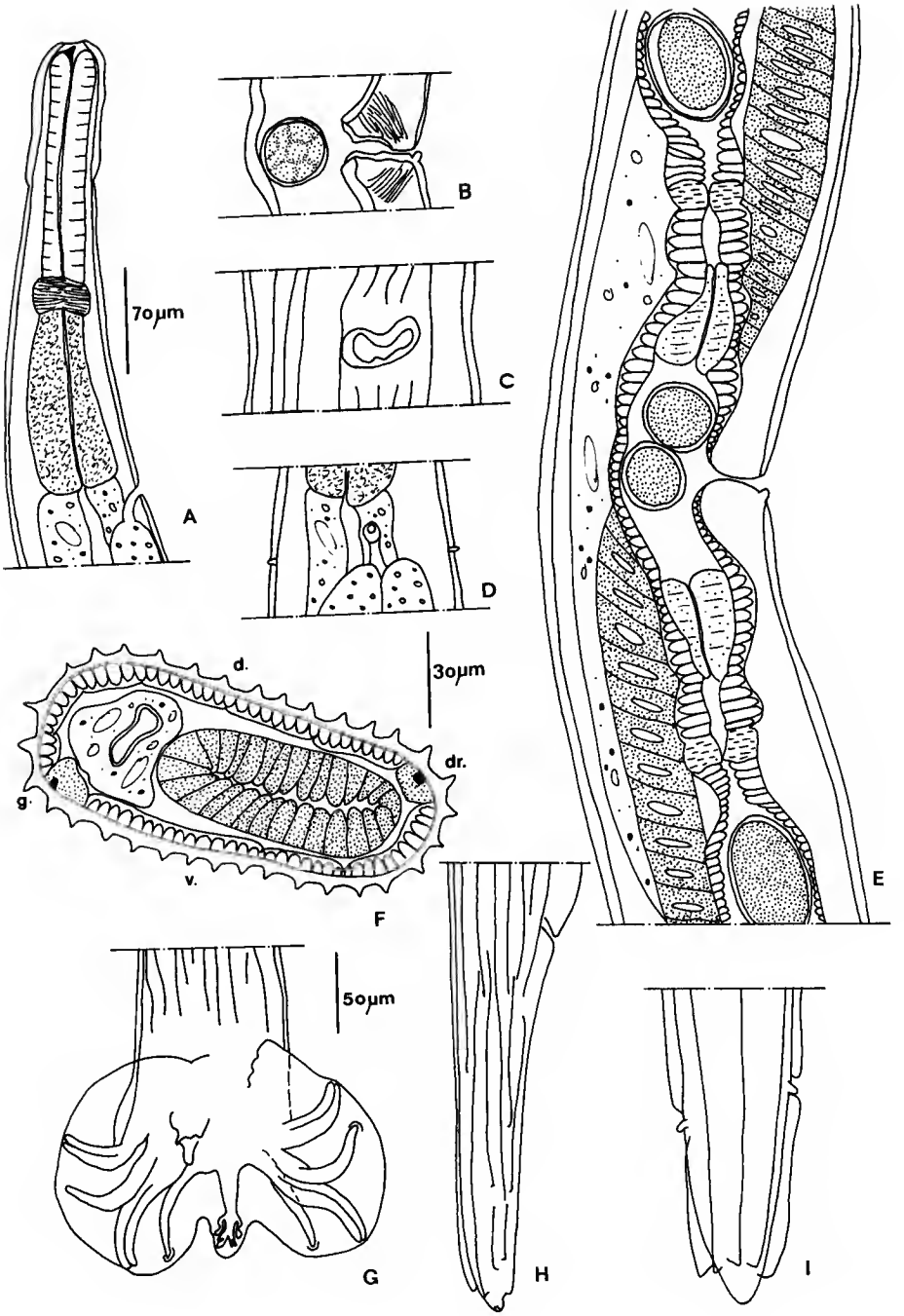
Origine géographique : Cupey, Porto Rico.

Collection : Julio GARCIA.

Identification : G. D. SCHMIDT.

FIG. 1. — *Oswaldocruzia lenteixeirai* Vigueras, 1938 chez *Eleutherodactylus portoricensis.* (Matériel de SCHMIDT et WITTAKER, 1975.) A-E, femelle : A, extrémité antérieure, vue latérale droite ; B, C, vulve, vues latérale droite et ventrale ; D, détail des deirides et du pore excréteur, vue ventrale ; E, ovéjecteur, vue latérale droite ; F, mâle, synlophe au milieu du corps ; G, *id.*, bourse caudale, vue ventrale avec disparition des crêtes cuticulaires ; H, femelle, queue, vue latérale droite ; I, femelle, extrémité caudale, vue ventrale, disparition des crêtes cuticulaires. Toutes les coupes sont orientées comme la figure 1 F. Échelle : A, E : 70 µm ; B-D, G, H : 50 µm ; F, I : 30 µm.

Oswaldocruzia lenteixeirai *Vigueras, 1938 from* Eleutherodactylus portoricensis. *(Original material from SCHMIDT & WITTAKER, 1975.) A-E, female: A, anterior extremity, right lateral view; B, Vulva, right lateral view; C,* id., *ventral view; D, deirids and excretory pore, ventral view; E, ovejector, right lateral view; F, male, synlophe at mid-body; G,* id. *caudal bursa, ventral view showing disappearance of cuticular ridges; H, female, tail, right lateral view; I, female, caudal extremity, ventral view, disapperance of cuticular ridges. All the body sections are orientated as fig. 1 F. Abbr.: d. = dorsal side; dr. = right side; v = ventral side. Scale: A, E: 70 µm; B-D, G, H: 50 µm; F, I: 30 µm.*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DESCRIPTION

Nématodes de grande taille, déroulés; pore excréteur situé postérieurement à la jonction œsophago-intestinale; deirides triangulaires, postérieures au pore excréteur (fig. 1 D); glandes excrétrices bien développées. Ailes cervicales absentes.

Tête : présence d'une vésicule céphalique et d'une grosse dent œsophagienne dorsale (fig. 1 A).

Synlophe (étudié chez le mâle en coupe transversale) : dans les deux sexes, corps parcouru longitudinalement par des crêtes cuticulaires continues pour la grande majorité d'entre elles. Certaines crêtes sont interrompues et remplacées par la naissance d'une autre crête. Chez le mâle, les crêtes cuticulaires disparaissent au niveau de la bourse caudale (fig. 1 G) et au niveau de la pointe caudale chez la femelle (fig. 1 H, I).

Chez le mâle, le nombre de crêtes est de 33 (16 crêtes dorsales, 17 crêtes ventrales) à 300 µm en avant de la bourse caudale. Toutes les crêtes sont orientées perpendiculairement à la paroi du corps, espacées régulièrement et de taille équivalente (fig. 1 F).

Mâle : morceau antérieur long de 2 000 µm, postérieur de 3 400 µm sur 160 µm de large dans sa partie moyenne. Vésicule céphalique haute de 92 µm sur 40 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 155 µm, 360 µm et 375 µm de l'apex. Œsophage long de 340 µm.

Bourse caudale de type 2-3 à tendance 2-1-2 : l'extrémité des côtes 4 étant coudée vers l'avant est plus proche de celle des côtes 3 que de celle des côtes 5. Côtes 2-3 d'une part et côtes 5-6 d'autre part jointives. Côtes 8 naissant à la racine de la côte dorsale et chevauchées par les côtes 6, sauf dans leur extrémité postérieure (type III). Côte dorsale divisée dans son quart postérieur en trois rameaux, les rameaux externes (côte 9) se détachant avant la division de la côte dorsale. Gubernaculum absent, cône génital de forme triangulaire haut de 30 µm sur 30 µm de large dans sa partie proximale, portant sur sa lèvre antérieure une large papille 0 et deux minuscules papilles 7 sur sa lèvre postérieure (fig. 1 G).

Spicules non disséqués, mais conformes à la descrition de SCHMIDT & WITTAKER (1975) : ailés, longs de 180 µm, à pointes complexes se divisant au tiers proximal de leur hauteur en trois branches principales; chaque branche est en forme de lame, chaque lame se termine en plusieurs pointes distales en forme de peigne.

Femelle : longue de 6 900 µm sur 190 µm dans sa partie moyenne. Vésicule céphalique haute de 85 µm sur 45 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 155 µm, 320 µm et 335 µm de l'apex. Œsophage long de 300 µm (fig. 1 A).

Didelphie, la vulve s'ouvre à 2 800 µm de la pointe caudale. *Vagina vera* long de 48 µm divisant le vestibule long de 270 µm en deux parties éqivalentes (fig. 1 E). Sphincter et trompe de chaque branche longs respectivement de 40 µm et 20 µm, branche utérine antérieure longue de 1 050 µm contenant 16 œufs au stade morula, branche utérine postérieure longue de 1 300 µm contenant 12 œufs au stade morula. Œufs hauts de 88 µm sur 45 µm de large. Queue longue de 240 µm sur 70 µm de large au niveau de l'anus, la longueur de l'épine caudale ne peut être donnée, cette dernière étant cassée (fig. 1 H, I).

Oswaldocruzia barusi n. sp.

Matériel type. — Mâle holotype, femelle allotype, Institute of Parasitology. Academy of Sciences of the Czech Republic, Helminthological Collections n° 646, a ; 2 mâles, 2 femelles paratypes, Institute of Parasitology, Academy of Sciences of the Czech Republic, Helminthological Collections n° 646, b.

Hôte : *Bufo empusus* Cope, 1862 (Bufonidae).

Localisation : intestin grêle.

Origine géographique : jardin botanique La Habana, Cuba.

Collection : Dr. V. Barus.

Identification : « *O. lenteixeirai* » V. Barus.

Description

Nématodes de grande taille présentant un tour de spire dans leur partie antérieure, le reste du corps étant déroulé ; pore excréteur de position variable, mais toujours situé dans le tiers postérieur de l'œsophage ; deirides postérieures au pore excréteur et de forme triangulaire, glandes excrétrices bien développées. Ailes cervicales présentes.

Tête : présence d'une vésicule céphalique et d'une petite dent œsophagienne dorsale. En vue apicale, on observe 6 papilles labiales externes, 2 amphides, 4 papilles céphaliques. Bouche triangulaire arrondie aux angles (fig. 2 B).

Synlophe (étudié chez un mâle et une femelle paratypes) : dans les deux sexes, corps parcouru longitudinalement par des crêtes cuticulaires continues à l'exception de quelques crêtes interrompues de façon irrégulière. La quasi-totalité des crêtes chez le mâle, les quatre cinquièmes chez la femelle naissent dans la région œsophagienne ; les crêtes disparaissent au niveau de la bourse caudale chez le mâle et au niveau des phasmides chez la femelle.

Au niveau de la jonction œsophago-intestinale, le nombre de crêtes est de 37 (20 dorsales, 17 ventrales) chez le mâle (fig. 2 C), de 39 (20 dorsales, 19 ventrales) chez la femelle (fig. 2 E). Au milieu du corps, le nombre de crêtes est de 38 (20 dorsales, 18 ventrales) chez le mâle (fig. 2 D) et de 48 (25 dorsales, 23 ventrales) chez la femelle (fig. 2 F).

Les crêtes sont espacées de façon régulière et sont de taille équivalente sauf dans la région œsophagienne où les deux crêtes latéro-ventrales proches des cordons latéraux sont légèrement plus grandes que les autres crêtes et forment des ailes cervicales visibles seulement en coupe transversale ; celles-ci naissent en arrière de la vésicule céphalique et disparaissent au niveau de la jonction œsophago-intestinale.

Toutes les crêtes sont orientées perpendiculairement à la paroi du corps, sauf les ailes cervicales dont la pointe est orientée ventralement.

Mâle holotype : long de 4 800 µm sur 125 µm de large dans sa partie moyenne. Vésicule céphalique haute de 75 µm sur 35 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 150 µ, 200 µm et 210 µm de l'apex. Œsophage long de 380 µm (fig. 2 A).

Bourse caudale de type 2-3 à tendance 2-1-2 : l'extrémité des côtes 4 étant coudée vers l'avant est plus proche de celle des côtes 3 que de celle des côtes 5. Côtes 8 naissant à la racine de la côte dorsale et chevauchées par les côtes 6 dans leur partie médiane (type II). Côte dorsale divisée dans son quart postérieur en trois rameaux, le rameau externe (côte 9) se détachant avant la division de la côte dorsale. Gubernaculum absent, cône génital de forme triangulaire haut de

30 µm sur 30 µm de large dans sa partie proximale, portant sur sa lèvre antérieure une large papille 0 et deux minuscules papilles 7 sur sa lèvre postérieure (fig. 2 M).

Spicules ailés, longs de 120 µm, à pointes complexes se divisant au tiers proximal de leur hauteur en trois branches principales chacune en forme de lame; chaque lame se termine en plusieurs pointes distales en forme de peigne (fig. 2 J-L).

Femelle allotype : longue de 7700 µm sur 120 µm dans sa partie moyenne. Vésicule céphalique haute de 70 µm sur 35 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 175 µm, 230 µm et 250 µm de l'apex. Œsophage long de 420 µm.

Didelphie, la vulve s'ouvre à 2850 µm de la pointe caudale. *Vagina vera* long de 45 µm divisant le vestibule long de 540 µm en deux parties équivalentes. Sphincter et trompe de chaque branche longs respectivement de 30 µm et de 20 µm (fig. 2 H). Branche utérine antérieure longue de 1 750 µm contenant 19 œufs au stade morula, branche utérine postérieure longue de 1750 µm contenant 25 œufs au stade morula. Œufs hauts de 60 µm sur 40 µm de large. Queue longue de 230 µm sur 50 µm de large au niveau de l'anus, pointe caudale longue de 19 µm (fig. 2 I).

O. anolisi Barus & Coy Otero, 1968

Matériel. — 2 mâles, 1 femelle, Institute of Parasitology, Academy of Sciences of the Czech Republic, Helminthological Collections, n° N-376.
Hôte : *Anolis equestris* Merrem, 1820 (Iguanidae).
Localisation : intestin grêle.
Origine géographique : Cuba.
Collection : Dr. V. Barus.
Identification : « *O. anolis* » V. Barus.

Description

Nématodes de grande taille et déroulés; pore excréteur situé très antérieurement (fig. 3 A); deirides au même niveau, filiformes et bien développées. Grandes ailes cervicales.

Tête : présence d'une vésicule céphalique et d'une petite dent œsophagienne dorsale.

Synlophe (étudié en coupe transversale chez un mâle) : dans les deux sexes, corps parcouru longitudinalement par des crêtes cuticulaires continues à l'exception de quelques crêtes interrompues de façon irrégulière. Les crêtes dorsales naissent en arrière de la vésicule céphalique

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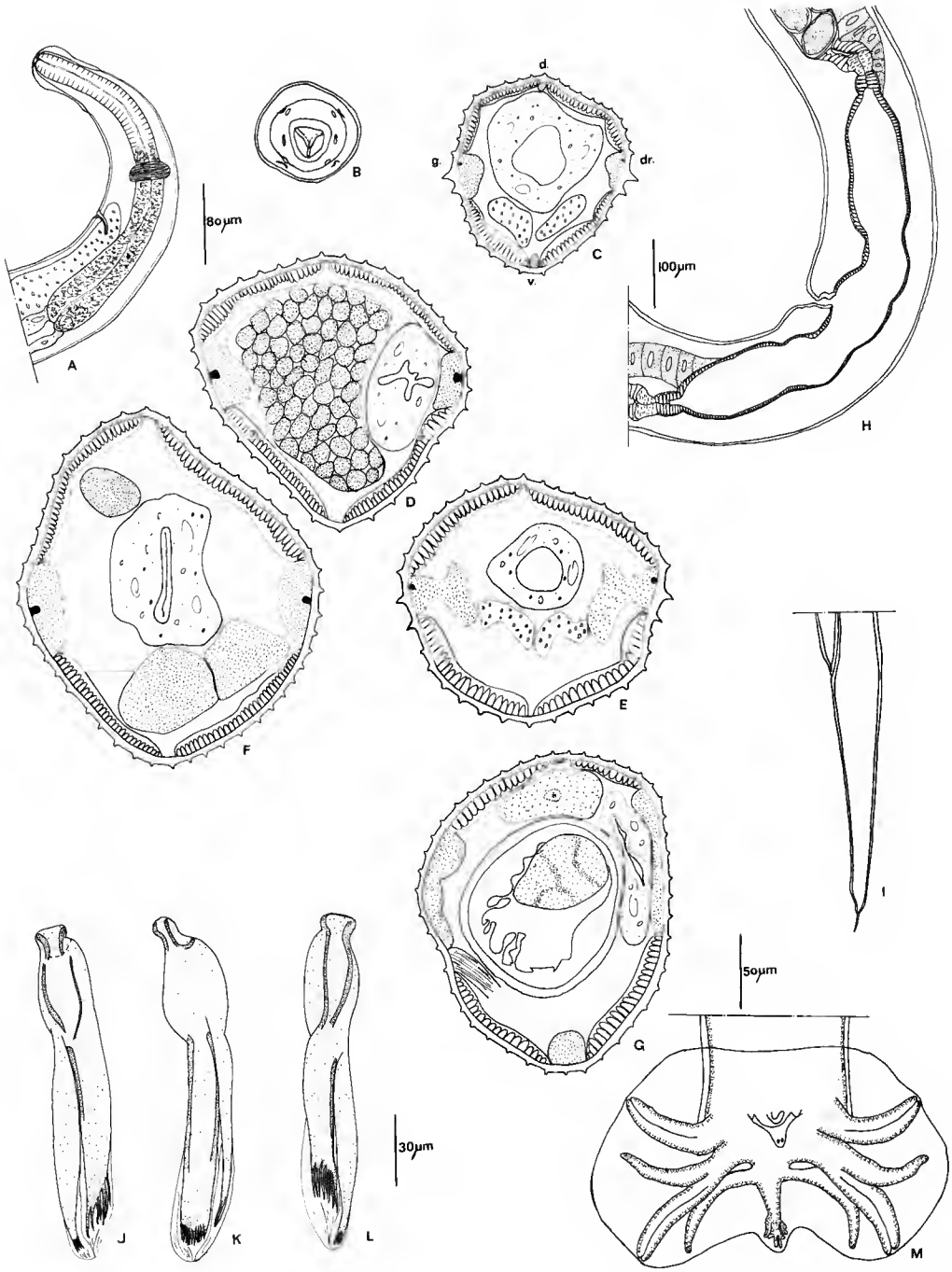
Fig. 2. — *Oswaldocruzia barusi* n. sp. chez *Bufo empusus*. A, mâle, partie antérieure, vue latérale gauche; B, femelle, tête, vue apicale; C, D, mâle, synlophe : C, au niveau de la jonction œsophago-intestinale; D, au milieu du corps; E-G, femelle, synlophe : E, au niveau de la jonction œsophago-intestinale; F, au milieu du corps, G, au niveau du vestibule; H, femelle, ovéjecteur, vue latérale gauche; I, femelle, queue, vue latérale gauche; J-L, mâle, spicule gauche disséqué : J, vue dorsale; K, vue externe; L, vue ventrale; M, mâle, bourse caudale, vue ventrale. Toutes les coupes sont orientées comme la figure 2 C. Échelle : A, I, M : 80 µm; B-G, J-L : 30 µm; H :100 µm.

Oswaldocruzia barusi *n. sp. from* Bufo empusus. *A, male, anterior extremity, left lateral view; B, female, head,* en face *view; C, D, male, synlophe: C, at the œsophago-intestinal junction level; D, at mid-body; E-G, female, synlophe: E, at the œsophago-intestinal junction level; F, at mid-body; G, at vestibule level; H, female, ovejector, left lateral view; I, female, tail, left lateral view; J-L, male, dissected left spicule: J, dorsal view; K, externo-lateral view; L, ventral view; M, male, caudal bursa, ventral view. All the body sections are oriented as fig. 2 C. Abbr.: d. = dorsal side, dr. = right side, g = left side, v. = ventral side. Scale: A, I, M: 80 µm; B-G, J-L: 30 µm; H: 100 µm.*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M

mais, sauf sur coupe transversale, elles ne deviennent visibles qu'au niveau de la jonction œsophago-intestinale. Les crêtes ventrales apparaissent à environ 180 µm en arrière de la fin de l'œsophage.

Le nombre de crêtes est de 13 (11 dorsales et 2 ailes latérales) dans la partie antérieure (fig. 3 B) et de 50 (25 dorsales, 25 ventrales) au milieu du corps (fig. 3 C). Les ailes cervicales naissent à la base de la vésicule céphalique et sont longues de 850 µm chez le mâle et de 950 µm chez la femelle. Chaque aile est composée d'une seule crête en position latéro-ventrale, haute de 28 µm dans sa partie la plus large. Les crêtes dorsales et ventrales sont orientées perpendiculairement à la paroi du corps, espacées régulièrement et de taille équivalente. Les ailes cervicales sont légèrement orientées dorso-ventralement.

Mâle : long de 8 350-9 700 µm sur 185-200 µm de large dans sa partie moyenne ; vésicule céphalique haute de 85-85 µm sur 50-60 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 140-150 µm, 190-200 µm et 210-220 µm de l'apex. Œsophage long de 440-480 µm (fig. 3 A).

Bourse caudale de type 2-3 à tendance 2-1-2 : l'extrémité des côtes 4 étant coudée vers l'avant est plus proche de celle des côtes 3 que de celle des côtes 5. Côtes 8 naissant à la racine de la côte dorsale, chevauchées par les côtes 6 dans leur partie médiane (type II). Côte dorsale divisée dans son quart postérieur en trois rameaux, le rameau externe (côte 9) se détachant avant la division de la côte dorsale. Gubernaculum absent, cône génital de forme triangulaire haut de 20 µm sur 20 µm de large dans sa partie proximale, portant sur sa lèvre antérieure une large papille 0 et deux minuscules papilles 7 sur sa lèvre postérieure (fig. 3 E).

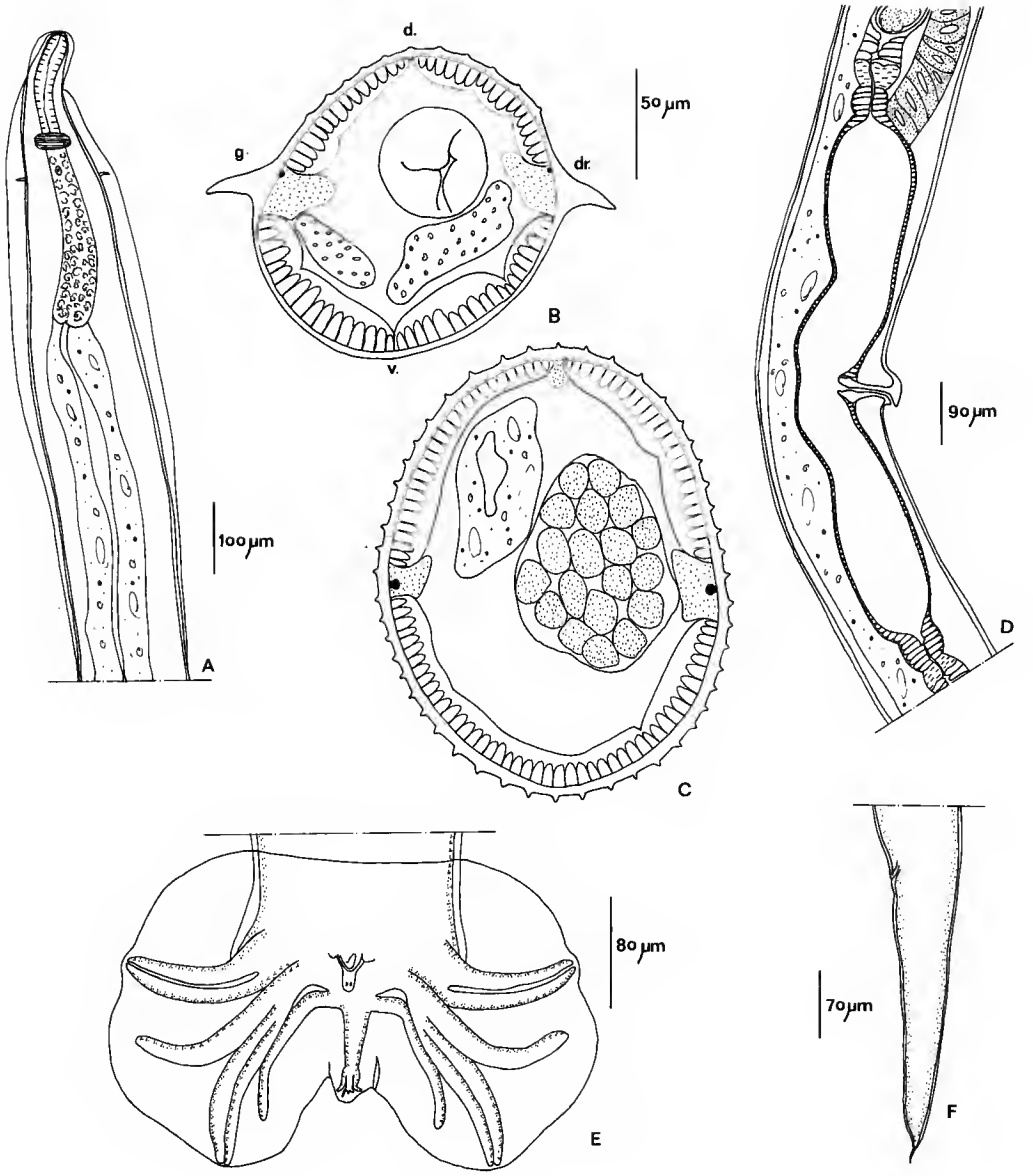
Spicules ailés, longs de 195-200 µm, à pointes complexes se divisant au tiers proximal de leur hauteur en trois branches principales, chacune en forme de lame ; chaque lame se termine en plusieurs pointes distales en forme de peigne.

Femelle : Longue de 13 100 µm sur 230 µm dans sa partie moyenne. Vésicule céphalique haute de 85 µm sur 55 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 170 µm, 260 µm et 280 µm de l'apex. Œsophage long de 430 µm.

Didelphie, la vulve s'ouvre à 4 400 µm de la pointe caudale. *Vagina vera* long de 50 µm divisant le vestibule, long de 600 µm, en deux parties équivalentes. Sphincter et trompe de chaque branche longs respectivement de 40 et 30 µm (fig. 3 D). Chaque branche utérine longue de 2 200 µm contient 30 œufs au stade morula hauts de 75 µm sur 40 µm de large. Queue longue de 280 µm sur 70 µm de large au niveau de l'anus, pointe caudale longue de 18 µm (fig. 3 F).

FIG. 3. — *Oswaldocruzia anolisi* Barus & Coy Otero, 1968 chez *Anolis equestris*. A, mâle, partie antérieure, vue ventrale ; B-C, mâle, synlophe : B, au niveau le plus large des ailes cervicales ; C, au milieu du corps ; D, femelle, ovéjecteur, vue latérale droite ; E, mâle, bourse caudale, vue ventrale ; F, femelle, queue, vue latérale gauche. Toutes les coupes sont orientées comme la figure 3 B. Échelle : A 100 µm ; B, C : 50 µm ; D : 90 µm E : 80 µm ; F : 70 µm.

Oswaldocruzia anolisi *Barus & Coy Otero, 1968, from* Anolis equestris. *A, male, anterior extremity, ventral view; B-C, male, synlophe: B, at the highest wide level of cervical alae; C, at mid-body; D, female, ovejector, right lateral view; F, female, tail, left lateral view. All the body sections are orientated as fig. 3 B. Abbr.: d. = dorsal side, dr. = right side, g. = left side, v. = ventral side. Scale: A: 100 µm; B, C: 50 µm; D: 90 µm; E: 80 µm; F: 70 µm.*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DISCUSSION

Les *Oswaldocruzia* parasites d'amphibiens et de reptiles des Antilles n'ont été décrits actuellement que de Cuba et de Porto Rico. Ils sont caractérisés par des spicules à trois branches principales, chacune en forme de lame, chaque lame se terminant en plusieurs pointes distales en forme de peigne. Ils constituent donc un groupe très homogène si bien que, depuis la mise en synonymie d'*O. anolisi,* une seule espèce, *O. lenteixeirai* est reconnue par tous les auteurs. Cependant, l'étude morphologique effectuée ci-dessus indique des différences importantes caractéristiques de chacun des lots examinés. Il est donc nécessaire de passer en revue les publications faites à ce sujet pour tenter d'éclaircir le problème.

— En 1938, la description *princeps* de VIGUERAS porte sur des parasites de *Hyla insula* (= *Hyla septentrionalis*) à Cuba. L'espèce est caractérisée par :

(1) l'absence d'ailes cervicales, tout au moins sur l'animal examiné sans coupe transversale du corps ;

(2) des côtes 6 et 8 dont la disposition est de type III ; des côtes 8 complètement chevauchées par les côtes 6 en vue ventrale, sauf à leur extrémité distale ;

(3) un vestibule très long (850-870 µm) avec une formation (?) glandulaire aux deux extrémités.

— En 1967, BARUS & MORAVEC pensent retrouver l'espèce chez le même hôte et dans la même région. Cependant, plusieurs caractères diffèrent de ceux de l'espèce précédente :

(1) les côtes 6 et 8 ont une disposition de type II, les côtes 6 chevauchant ventralement les côtes 8 uniquement dans leur partie médiane ;

(2) les côtes 5 et 6 ne sont pas jointives, mais leurs extrémités divergent. En outre, les côtes 5, 6 et 8 sont de longueur équivalente ;

(3) le vestibule est dépourvu de formations particulières à ses extrémités ;

(4) la vulve est entourée de deux becs cuticulaires, l'un antérieur, l'autre postérieur.

Ces Nématodes nous paraissent donc différents de ceux de VIGUERAS et nous proposons de les nommer *Oswaldocruzia moraveci* n. sp. (= *O. lenteixeirai sensu* BARUS & MORAVEC, 1967, *nec* VIGUERAS, 1938).

— En 1968, BARUS & COY OTERO décrivent *O. anolisi* chez *Anolis equestris* de Cuba. Le matériel décrit ci-dessus correspond au matériel original, et les caractéristiques morphologiques correspondent à celles indiquées dans la description originale ; plusieurs éléments permettent de différencier *O. anolisi* des deux autres espèces :

(1) présence d'ailes cervicales simples et bien développées ;

(2) présence de becs cuticulaires périvulvaires, l'antérieur important, le postérieur faible ;

(3) deirides allongées et bien développées chez *O. anolisi*, arrondies et petites chez *O. lenteixeirai ;*

(4) crêtes cuticulaires ventrales absentes dans la partie antérieure du corps chez *O. anolisi*, présentes chez *O. lenteixeirai ;*

(5) côtes bursales 8 chevauchées par les côtes 6 dans leur portion médiane (type II) chez *O. anolisi* et non dans leur deux tiers proximaux (type III) chez *O. lenteixeirai.*

La validité de l'espèce *O. anolisi* semble donc ne faire aucun doute.

— En 1969, BARUS & COY OTERO et, en 1970, COY OTERO signalent la présence d'*O. anolisi* chez de nombreux lézards Iguanidae et Teiidae de Cuba.

— En 1972, BARUS identifie à *O. lenteixeirai* les parasites de différentes espèces d'*Eleutherodactylus* de Cuba, mais signale que la longueur des spicules (87-133 µm) est inférieure à celle des parasites de *Hyla* ou de *Bufo* (124-182 µm).

— En 1973, BARUS identifie à *O. lenteixeirai* les parasites de différentes espèces de *Bufo* de Cuba, et précise quelques éléments morphologiques (ailes cervicales très petites, synlophe avec 34 à 36 crêtes cuticulaires).

— En 1975, SCHMIDT & WHITTAKER identifient *O. lenteixeirai* chez un *Eleutherodactylus* de Porto Rico et fournissent quelques éléments morphologiques supplémentaires. C'est leur matériel que nous avons utilisé ci-dessus pour redécrire l'espèce. Il eut été plus satisfaisant de s'appuyer sur le matériel de BARUS et MORAVEC de 1967 puisque l'hôte et la géographie coïncident avec ceux de la description originale, mais nous savons qu'un même hôte peut héberger plusieurs espèces différentes d'*Oswaldocruzia*. En outre et surtout, les différences morphologiques entre la description de VIGUERAS et celle de BARUS & MORAVEC sont considérables alors qu'aucun élément important ne sépare le matériel de SCHMIDT & WHITTAKER de la description de VIGUERAS.

En 1978, BARUS & COY OTERO rapportent la présence d'*Oswaldocruzia* chez plusieurs serpents de Cuba, mais bien que ces parasites aient tous de grandes ailes cervicales, les auteurs proposent la synonymie de leur espèce *O. anolisi* avec *O. lenteixeirai* ce qui, comme il est indiqué plus haut, nous semble inexact.

Enfin, dans le présent article, des spécimens parasites de *Bufo empusus* de Cuba, qui avaient été rattachés primitivement à *O. lenteixeirai* nous paraissent s'en différencier par les ailes cervicales, la bourse caudale, les spicules et la structure du vestibule et nous avons proposé de les nommer *O. barusi* n. sp.

En conclusion, nous estimons que les *Oswaldocruzia* de Cuba et de Porto Rico, qui sont les seuls étudiés actuellement aux Antilles, comportent au moins quatre espèces distinctes qui peuvent être reconnues par les caractères suivants.

O. lenteixeirai Vigueras, 1938 : ailes cervicales absentes ; 32-38 crêtes cuticulaires au milieu du corps chez le mâle, 52-58 chez la femelle ; bourse caudale avec des côtes 8 naissant à la racine de la côte dorsale et chevauchées par les côtes 6 dans leurs deux tiers proximaux (type III) côtes 2-3 d'une part et côtes 5-6 d'autre part jointives ; longueur des lames des spicules subégales ; languettes vulvaires absentes ; vestibule pourvu de formations distales.

O. moraveci n. sp. (= *O. lenteixeirai sensu* BARUS & MORAVEC, 1967) : ailes cervicales absentes ; nombre de crêtes cuticulaires inconnu ; bourse caudale avec des côtes 8 naissant sur la côte dorsale et chevauchées par les côtes 6 dans leur partie médiane (type II) ; côtes 2-3 jointives ; côtes 5-6 divergentes dans leur tiers distal ; longueur des lames des spicules subégales ; présence de languettes vulvaires ; vestibule dépourvu de formations distales.

O. anolisi Barus & Coy Otero, 1968 : ailes cervicales très larges ; absence de crêtes cuticulaires ventrales dans la partie antérieure du corps ; 50 crêtes cuticulaires au milieu du corps chez le mâle ; côtes 2-3 séparées et côtes 5-6 jointives ; côtes 8 naissant sur la côte dorsale et chevauchées par les côtes 6 dans leur partie médiane (type II) ; longueur des lames des spicules subégales ; présence d'une languette prévulvaire ; vestibule dépourvu de formations distales.

O. barusi n. sp. (= *O. lenteixeirai sensu* BARUS, 1973) : ailes cervicales peu développées, indiquées seulement par les deux paires de crêtes latérales légèrement plus grandes que les autres ; 38 crêtes cuticulaires au milieu du corps chez le mâle, 48 chez la femelle ; la disposition des côtes 6 et 8 est de type II ; lame externe des spicules plus longue que les deux lames internes ; languettes vulvaires absentes ; vestibule dépourvu de formations distales.

Remerciements

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Oswaldocruzia peruensis n. sp. (Nematoda,Trichostrongylina, Molineoidea), parasite d'un Iguanidae du Pérou

par Badreddine BEN SLIMANE, Manfred VERHAAGH
et Marie-Claude DURETTE-DESSET

Résumé. — Description d'*Oswaldocruzia peruensis* n. sp., parasite de *Stenocercus roseiventris* du Pérou. L'espèce appartient aux *Oswaldocruzia* néotropicaux caractérisés : (1) par des spicules à trois branches principales (lame, fourche et sabot) avec division de la fourche en deçà de son tiers distal et division de la lame en « peigne » à son extrémité distale ; (2) par une disposition relative des côtes 6, 8 et dorsale de type II. La seule espèce proche, *Oswaldocruzia vaucheri* Ben Slimane & Durette-Desset, 1993, parasite d'un Leptodactylidae d'Équateur, s'en distingue par l'existence de crêtes et non d'ondulations cuticulaires et par la forme des ailes cervicales.

Mots-clés. — *Oswaldocruzia peruensis* n. sp., Nematoda, Trichostrongylina, Molineoidea, Iguanidae, *Stenocercus*, Pérou.

***Oswaldocruzia peruensis* n. sp. (Nematoda, Trichostrongylina, Molineoidea), parasite of an Iguanidae from Peru**

Abstract. — Description of *Oswaldocruzia peruensis* n. sp. parasite of *Stenocercus roseiventris* from Peru. *O. peruensis* belongs to the group of *Oswaldocruzia* spp. characterized by : (1) three spicular branches (blade, fork and shoe) with the fork subdivided at its distal extremity and the blade subdivided into many processes ; and (2) by a type II bursal pattern of rays 6, 8 and dorsal. The only closely related species, *O. vaucheri* Ben Slimane & Durette-Desset, 1993, a parasite of leptodactylids in Ecuador, differs by the presence of cuticular crests which undulate and by the shape of the cervical alae.

Keywords. — *Oswaldocruzia peruensis* n. sp., Nematoda, Trichostrongylina, Molineoidea, Iguanidae, *Stenocercus*, Peru.

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INTRODUCTION

Au cours d'un travail de terrain sur les fourmis à la station biologique de Panguana (9°37'S, 74°56'W), Rio Yuya pichis, Departamento Huanuco, Pérou, l'un de nous a capturé un *Stenocercus roseiventris* (Iguanidae) dans un vaste piège posé en lisière de la forêt primaire humide. Outre des Nématodes Ascarides non encore étudiés, trouvés dans l'estomac, l'intestin grêle et le colon, nous avons trouvé 14 Nématodes Trichostrongles dans le rectum. Il s'agit d'une espèce non connue d'*Oswaldocruzia* Travassos, 1917, que nous décrivons ci-après.

MATÉRIEL ET MÉTHODES

L'estomac et l'intestin de l'hôte ont été séparés du corps et fixés, non ouverts, à l'alcool à 70° au moment de la capture en octobre 1984. Les parasites ont été extraits au printemps 1993 et conservés dans l'alcool à 70°. Le matériel étudié est déposé dans les collections du Muséum national d'Histoire naturelle de Paris (MNHN) et du Staatliches Museum für Naturkunde Karlsruhe (SMNK). Le synlophe est étudié selon la méthode de DURETTE-DESSET (1985); la nomenclature utilisée pour la bourse caudale est celle de DURETTE-DESSET & CHABAUD (1981); concernant la description des côtes 6, 8 et 9 (côte dorsale), celle de DURETTE-DESSET, NASHER & BEN SLIMANE (1992); concernant les spicules celle de BEN SLIMANE, DURETTE-DESSET & CHABAUD (1993).

La nomenclature utilisée au-dessus du groupe famille est celle de DURETTE-DESSET & CHABAUD (1993). Les mensurations de l'holotype et de l'allotype sont données en premier suivies de celles des extrêmes des paratypes entre parenthèses.

DESCRIPTION

Oswaldocruzia peruensis n. sp.

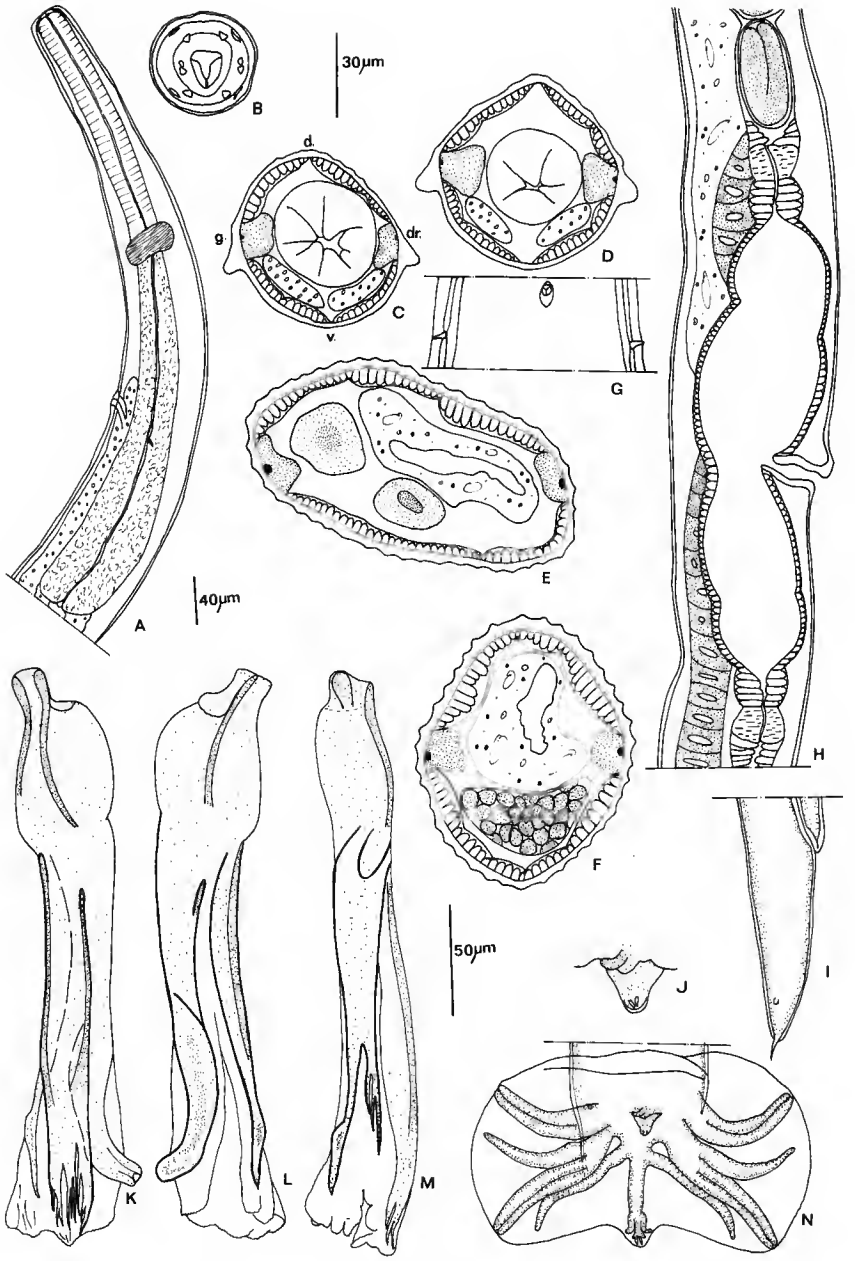
MATÉRIEL-TYPE. — Mâle holotype, femelle allotype, MNHN 758 MDa; 3 mâles, 5 femelles paratypes, MNHN 758 MDb. 2 mâles, 2 femelles paratypes SMNK – Ver 172.
Hôte : *Stenocercus roseiventris* Duméril et Bibron, 1837 (Iguanidae).
Localisation : rectum.
Origine géographique : Panguana, Pérou.
Collecteur : M. VERHAAGH ; date de récolte : 7 octobre 1984.

Nématodes ne présentant pas d'enroulement du corps. Vésicule céphalique présente; pore excréteur situé dans le tiers postérieur de l'œsophage, deirides peu développées situées en arrière du pore excréteur, glandes excrétrices bien développées. Présence d'ailes cervicales. Synlophe formé d'ondulations dépourvues de soutien chitinoïde.

Tête : vésicule céphalique simple. En vue apicale, on observe deux amphides, six papilles labiales externes dont les deux latérales sont accolées aux amphides, quatre papilles céphaliques et une dent œsophagienne dorsale. Bouche triangulaire (fig. 1 B).

FIG. 1. — A : mâle, partie antérieure, vue latérale gauche. B : mâle, tête, vue apicale. C-F : synlophe ; C : mâle, coupe transversale en arrière des deirides ; D : femelle, *id.* ; E : femelle, coupe transversale au milieu du corps ; F : mâle, *id.* G : mâle, détail du pore excréteur et des deirides, vue ventrale. H : femelle, ovéjecteur, vue latérale droite. I : femelle, queue, vue latérale droite. J : mâle, cône génital, vue ventrale. K-M : spicule gauche disséqué ; K : vue externo-latérale ; L : vue interne ; M : vue ventrale. N : mâle, bourse caudale, vue ventrale. Toutes les coupes transversales sont orientées comme la fig. 1 C. Abréviations : d. = dos, dr. = droite, g. = gauche, v. = ventre. Échelle : A, H, I, N = 40 µm ; B, E, J, K, L, M = 30 µm ; C, D, F, G = 50 µm.

A : male, anterior part, left lateral view. B: male, head, en face *view. C-F: synlophe; C: male, transversal section posterior to the deirides; D : female,* id.; *E: female, synlophe at mid-body; F: male,* id. *G: male, excretory pore and deirids, ventral view. H: female, ovejector, right lateral view. I: female, tail, right lateral view. J: male, genital cone ventral view. K-M: dissected left spicule; K: externo-lateral view; L : interno-lateral view; M: ventral view. N: male, caudal bursa, ventral view. All the body sections are orientated as the fig. 1 C. Abbreviations: d. = dorsal side; dr. = right side; g. = left side; v. = ventral side. Scale: A, H, I, N = 40 µm; B, E, J, K, L, M = 30µm; C, D, F, G = 50 µm.*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Synlophe (étudié, en coupe transversale, chez un mâle et une femelle) : dans les deux sexes, corps parcouru longitudinalement par des lignes cuticulaires sous forme d'ondulations visibles seulement en coupe transversale, sauf dans la partie antérieure où les ondulations dorsales sont plus fortes, donc visibles *in toto*. Les ondulations dorsales naissent à la base de la vésicule céphalique tandis que les ventrales n'apparaissent qu'à environ 300 µm en arrière de la vésicule céphalique chez le mâle et 270 µm en arrière de la jonction œsophago-intestinale chez la femelle. Toutes les ondulations disparaissent au niveau de la bourse caudale chez le mâle et au niveau des phasmides chez la femelle.

Les ailes cervicales, arrondies en coupe transversale, naissent à 90-130 µm (mâle), 70-150 µm (femelle) en arrière de la vésicule céphalique et sont longues de 410-540 µm (mâle), 340-510 µm (femelle). En coupe transversale, la hauteur maximale de l'aile se situe entre le niveau de l'anneau nerveux et celui du pore excréteur. Cette hauteur est de 12,5 µm chez le mâle (fig. 1 C) et 13,8 µm chez la femelle (fig. 1 D). Les ailes sont en position latero-ventrale et orientées vers la face ventrale.

Au milieu du corps, le nombre d'ondulations est de 37 chez le mâle (18 dorsales, 19 ventrales) (fig. 1 F) et de 43 chez la femelle (22 dorsales et 21 ventrales) (fig. 1 E).

Mâle : long de 6 950 (7 500-8 500) µm sur 100 (110-130) µm de large dans sa partie moyenne. Vésicule céphalique simple, haute de 90 (90-100) µm sur 40 (50-50) µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 200 (220-240) µm, 350 (390-410) µm et 370 (410-430) µm de l'apex. Œsophage long de 520 (530-620) µm (fig. 1 A).

Bourse caudale de type 2-3 à tendance 2-1-2, c'est-à-dire que les extrémités des côtes 4 étant dirigées vers l'avant sont plus proches de celles des côtes 3 que de celles des côtes 5. Côtes 2-3 d'une part et 5-6 d'autre part, jointives; disposition relative des côtes 6, 8 et 9 (côte dorsale) de type II, les côtes 8 naissant apicalement sur la côte dorsale et étant chevauchées ventralement par les côtes 6 sur leur partie médiane. Les côtes 9 se détachent de la côte dorsale avant la division de celle-ci en deux rameaux dont l'interne est le plus long (fig. 1 N). Gubernaculum absent, cône génital haut de 20 sur 20 µm de large dans sa partie proximale, portant sur sa lèvre antérieure une grosse papille 0 et deux minuscules papilles 7 sur sa lèvre postérieure (fig. 1 J).

Spicules subégaux, longs de 180 (200-250) µm, divisés en deçà de leur tiers proximal en trois branches : lame, fourche et sabot; la lame se divise en «peigne» d'abord en 3 rameaux qui se ramifient en 9 pointes (fig. 1 K). Sur les trois spicules disséqués, la fourche se divise à 23, 25 et 26% de la hauteur totale des spicules, en 2 branches de longueur inégale et de forme différente, l'interne étant plus courte et ramifiée (fig. 1 M).

Femelle : longue de 10 100 (8 700-13 550) µm sur 120 (100-150) µm de large dans sa partie moyenne. Vésicule céphalique haute de 90 (80-100) µm sur 40 (40-50) µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 220 (200-250) µm, 390 (350-410) µm et 410 (370-450) µm de l'apex. Œsophage long de 550 (510-620) µm.

Didelphie. La vulve s'ouvre à 3500 (2 800-4 450) µm de la pointe caudale. *Vagina vera* long de 50 (50-50) µm divisant le vestibule long de 370 (320-390) µm en deux parties inégales, l'antérieure étant plus grande de 30 (10-30) µm. Sphincter, trompe et branche utérine antérieurs longs respectivement de 30 (30-30) µm, 30 (25-30) µm et 2 000 (1 750-2 650) µm. Sphincter, trompe et branche utérine postérieurs longs respectivement de 30 (30-30) µm, 30 (25-30) µm et

2 100 (1 500-2 700)µm. Les œufs, embryonnés, hauts de 90 (80-85) µm sur 40 (40-45) µm de large, sont au nombre de 40 (20-45) dans la branche utérine antérieure et 38 (20-50) dans la postérieure (fig. 1 H). Queue longue de 180 (160-240) µm sur 60 (60-75) µm de large au niveau de l'anus, se terminant par une pointe caudale longue de 20 (16-20) µm (fig. 1 I).

DISCUSSION

Les spécimens de l'iguane présentent les principaux caractères du genre *Oswaldocruzia* Travassos, 1917 et sont caractérisés, comme la grande majorité des espèces néotropicales de la sous-zone guyano-brésilienne, par des spicules à trois branches principales dont la fourche est divisée en deçà de son tiers postérieur et dont la lame se termine en «peigne».

Parmi ces espèces, seule *O. vaucheri* décrit par BEN SLIMANE et DURETTE-DESSET, 1993, parasite d'un Leptodactylidae d'Équateur, possède, comme nos spécimens, une vésicule céphalique simple, une disposition des côtes 6, 8 et 9 (côte dorsale) de type II et des ailes cervicales. Elle s'éloigne de l'espèce du Pérou par la présence de crêtes cuticulaires bien marquées, même si elles sont dépourvues de soutien chitinoïde et par des ailes cervicales en forme de demi-lune.

Nous séparons donc les spécimens de l'Iguanidae dans une nouvelle espèce que nous proposons de nommer *Oswaldocruzia peruensis* n. sp.

Remerciements

Le second auteur est reconnaissant au Pr H. W. KOEPCKE et à sa fille le Dr J. DILLER de l'avoir autorisé à rester au Panguana pendant plus de deux ans et au Directeur général de la Forêt et de la Faune de Lima de lui avoir accordé l'autorisation de faire des recherches au Pérou. Le travail au Panguana a été financé par une subvention de la DAAD (German Academic Exchange Service).

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n° 1-2 : 83-86.

Identity of the Antarctic mite *Gainia nivalis* Trouessart (Acari, Nanorchestidae)

by Mark JUDSON

Abstract. — The types of *Gainia nivalis* Trouessart, 1914, from Petermann Island (Antarctic Peninsula), have been re-examined and a lectotype designated. *Gainia* Trouessart, 1914, is confirmed to be a junior subjective synonym of *Nanorchestes* Topsent and Trouessart, 1890. *Nanorchestes nivalis* (n. comb.) is a senior subjective synonym of *N. gressitti* Strandtmann, 1982 (n. syn.). Authorship of the family name Nanorchestidae is attributed to BERLESE, 1913.

Keywords. — Acari, *Nanorchestes, Gainia,* Antarctic.

Identité de l'acarien antarctique *Gainia nivalis* Trouessart (Acari, Nanorchestidae)

Résumé. — Les types de *Gainia nivalis* Trouessart, 1914, provenant de l'île Petermann (Péninsule Antarctique), ont été réexaminés et un lectotype désigné. *Gainia* Trouessart, 1914, est confirmé comme synonyme subjectif de *Nanorchestes* Topsent et Trouessart, 1890. *Nanorchestes gressitti* Strandtmann, 1982, est un synonyme subjectif de *N. nivalis* (n. comb., n. syn.). La paternité du nom de famille Nanorchestidae est attribuée à BERLESE, 1913.

Mots-clés. — Acariens, *Nanorchestes, Gainia*, Antarctique.

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INTRODUCTION

Mites of the cosmopolitan genus *Nanorchestes* Topsent & Trouessart (Nanorchestidae) form an important and characteristic component of the Antarctic fauna. Of the thirty-or-so species known world-wide, fourteen have been recorded from the Antarctic and sub-Antarctic regions (PUGH, 1993)[1], including the southernmost-living terrestrial arthropod (GRESSITT, 1967*a*).

The genus *Gainia* was created by TROUESSART (1914) for a new species, *Gainia nivalis* Trouessart, collected from Petermann Island off the coast of the Antarctic Peninsula. TROUESSART placed it in the Alycinae, which at that time contained the genera *Alycus* C. L. Koch, *Michaelia* Berlese, *Nanorchestes* and *Hybalicus* Berlese, stating that the new genus was closest to *Michaelia* (= *Bimichaelia* Thor). WILLMANN (in THOR & WILLMANN, 1941) suggested that *Gainia* might

1. This high proportion of Antarctic species is probably due to the fact that relatively little attention has been paid to the systematics of *Nanorchestes* species from other regions of the world.

be a synonym of *Nanorchestes*, a view reiterated by STRANDTMANN (1967) and PUGH (1993). THERON (1975) listed *Gainia* as a synonym of *Nanorchestes*, without comment.

Because of the inadequacy of the original description, the identity of *Gainia nivalis* has remained doubtful and there have been no further records of this species. GRESSITT (1967*b*: 382) suggested that *G. nivalis* might be identical with *Nanorchestes antarcticus* Strandtmann. In fact the latter has since been shown to be a polyphyletic assemblage of species (STRANDTMANN, 1982). Fortunately, TROUESSART's types are still present in the Muséum national d'Histoire naturelle, Paris, and a re-examination of this material shows that it is conspecific with *Nanorchestes gressitti* Strandtmann, 1982, one of the species previously confused with *N. antarcticus*.

Family NANORCHESTIDAE Berlese, 1913[2]
Genus **NANORCHESTES** Topsent & Trouessart, 1890

Nanorchestes TOPSENT & TROUESSART, 1890: 892 (type species *Nanorchestes amphibius* Topsent & Trouessart, 1890, by monotypy).

Gainia TROUESSART, 1914: 13-14 (type species *Gainia nivalis* Trouessart, 1914, by monotypy); THOR & WILLMANN, 1941: 148. Synonymized by THERON, 1975: 1.

REMARKS

Although *Gainia* is clearly a synonym of *Nanorchestes* as currently recognized, it might perhaps be revalidated in the future. *Nanorchestes* is a relatively large genus, including about 30 species, and might usefully be split into smaller generic or subgeneric taxa. MCDANIEL & BOLEN (1981) named a closely related genus, *Neonanorchestes*, for two North American species with clavate trichobothria *nb*. The validity of *Neonanorchestes* was questioned by BOOTH (1984), but the recent discovery of alternating calyptostasy in this genus (KETHLEY, 1991) suggests that it may be monophyletic. This leaves, however, the question as to whether *Nanorchestes* itself represents a natural group. As both the clavate trichobothria and the alternating calyptostasis of *Neonanorchestes* probably represent autapomorphies, it is possible that the recognition of this genus leaves *Nanorchestes* paraphyletic. At least one species currently placed in *Nanorchestes* – *N. siculus* (Berlese, 1910) – has clavate trichobothria, though its nymphs are as yet unknown.

Nanorchestes nivalis (Trouessart) n. comb.

Gainia nivalis TROUESSART, 1914: 14, Figs. 8-9; THOR & WILLMANN, 1941: 148-149, Fig. 206; DALENIUS, 1965: 421; GRESSITT, 1967*a*: 5, Table 2; GRESSITT, 1967*b*: 382; STRANDTMANN, 1967: 79; BLOCK, 1992: 161, 167; PUGH, 1993: 339.

Nanorchestes antarcticus (not Strandtmann), STRANDTMANN, 1967: 7, Fig. 14g (in part, "variant 4" from South Orkney Islands).

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2. Although authorship of the family Nanorchestidae has traditionally been accredited to GRANDJEAN (1937), the tribe Nanorchestini was proposed by BERLESE (1913: 17), who is therefore the author of the co-ordinate family name (ICZN Code, article 36).

Nanorchestes gressitti Strandtmann, 1982d: 253-256, Figs 1-17; CENXUAN & SHIMADA, 1991: 326, 330, Fig. 1D; PUGH, 1993 : 338. **New synonymy**.

MATERIAL EXAMINED. — Lectotype ♂ (MNHN, slide 63B9), paralectotypes 2 ♂, 1 ♀ (MNHN, slide 45C13) and 8 other specimens (MNHN, slides 45B2 and 45C12), all labelled "Charcot, sur neige rouge, I. Petermann, Antarctique." The original identification labels read : "*Gainia nivalis* n. g.– n. sp. (Rostre. Type)" [45B2]; "*Gainia nivalis* Trt. (Téguments)" [45C12]; and "*Gainia nivalis* Trt. (Profil)" [45C13]; each label is also marked with a cross in red pencil.

REMARKS

Although only one of the three original slides was labelled "type", it is clear that all of the specimens are from the original collection and should be regarded as syntypes. The name 'Charcot' on the labels refers to Dr J.-B. CHARCOT, leader of the Second French Antarctic Expedition (1908-1910). Petermann Island (65°10'S 64°10'W) was visited by the expedition in March 1909, where the mites were collected by the expedition's biologist, L. GAIN (TROUESSART, 1914).

The types were in poor condition when TROUESSART received them, and have deteriorated since. They were strongly compressed beneath the coverslips and the mountant had dried out around them, so that little other than their silhouettes can be seen. The four specimens (3 ♂, 1 ♀) on slide 45C13 were temporarily de-mounted and examined in lactic acid; one of these males has been selected as the lectotype and is now mounted on a separate slide (63B9).

Although a complete examination was not possible, sufficient details became visible to show that the types are conspecific with *Nanorchestes gressitti* Strandtmann, known from Anvers Island (Antarctic Peninsula), South Shetland Is, South Orkney Is, South Sandwich Is and South Georgia Is. Apparent discrepancies between the descriptions of TROUESSART (1914) and STRANDTMANN (1982) are due to misinterpretations by TROUESSART. In particular, the form of the chelicerae, trichobothria and the apoteles of the legs are all typical of *Nanorchestes*. The types of *nivalis* agree with STRANDTMANN's description (as *N. gressitti*) in the following :

1. Size : TROUESSART gave the body length as being 0.5 mm, presumably including the gnathosoma. The idiosomal length of the 12 specimens (probably mostly adult) varies from about 320 to 450 µm, though most are between 360 and 400 µm long. STRANDTMANN (1982) records a range of 270-400 µm for adults. Allowing for the compression of the types of *nivalis*, these figures are reasonably similar;

2. "Wings" of naso narrow and widely separated;

3. Trichobothrium *na* long (80 µm), strongly ciliated on distal third; *nb* long (65 µm), finely ciliated, without apical branches;

4. Cheliceral seta *cha* bifurcate, branches roughly equal in length;

5. Anterior seta of telofemur I with only a few, reduced cilia at apex;

6. Tarsus III with 8 setae.

These characters, at least in the case of the specimens examined in detail, rule out the possibility that types of *nivalis* are conspecific with *N. berryi* Strandtmann, a species recorded as being sympatric with *N. gressitti* at two localities on the nearby Anvers Island by STRANDTMANN (1982). However, as it is not possible to state with certainty that the remaining types are all conspecific, it seems prudent to designate a lectotype for *nivalis*.

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n° 1-2 : 87-94.

Description de *Bordea*, nouveau genre endémique d'araignées des Pyrénées (Araneae : Linyphiidae)

par Robert BOSMANS

Résumé. — Le nouveau genre *Bordea*, endémique des Pyrénées, est créé pour les espèces *Lepthyphantes cavicola* (Simon) et *Lepthyphantes negrei* Dresco. Il se distingue de *Lepthyphantes* principalement par les denticules du tibia de la patte-mâchoire du mâle et le crochet long, non plié de la femelle. Les synonymes et combinaisons suivants sont proposés : *Lepthyphantes coiffaiti* Denis, 1953 = *Lepthyphantes cavicola* (Simon, 1884) n. syn. = *Bordea cavicola* (Simon) n. comb. *Lepthyphantes ecclesiasticus* Denis, 1959 = *Lepthyphantes negrei* Dresco, 1951 n. syn. = *Bordea negrei* (Dresco) n. comb.

Mots-clés. — Linyphiidae, *Lepthyphantes*, Pyrénées.

Description of *Bordea*, a new endemic spider genus from the Pyrénées (Araneae : Linyphiidae)

Abstract. — To receive the species *Lepthyphantes cavicola* (Simon) and *Lepthyphantes negrei* Dresco, the new genus *Bordea* is created, endemic to the Pyrénées, distinguished from *Lepthyphantes* by the tibial tubercles in the male palp, and by the long, unfolded scape in the female. The following new synonyms and combinations are proposed: *Lepthyphantes coiffaiti* Denis, 1953 = *Lepthyphantes cavicola* (Simon, 1884) n. syn. = *Bordea cavicola* (Simon) n. comb.; *Lepthyphantes ecclesiasticus* Denis, 1959 = *Lepthyphantes negrei* Dresco, 1951 n. syn. = *Bordea negrei* (Dresco) n. comb.

Keywords. — Linyphiidae, *Lepthyphantes*, Pyrénées.

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INTRODUCTION

Considéré polyphylétique, le genre *Lepthyphantes* Simon compte actuellement environ 440 espèces. SAARISTO & TANASEVITCH (1992) ne distinguèrent pas moins de 31 groupes d'espèces. Malgré la création de nouveaux genres pour certains groupes (ESKOV & MARUSIK, 1992 : *Parawubanoides;* TANASEVITCH, 1992 : *Himalaphantes*, *Incestophantes*, *Herbiphantes* et *Crispiphantes;* WUNDERLICH, 1993 : *Megalepthyphantes*) ou une meilleure délimination de certains complexes d'espèces (HELSDINGEN *et al.*, 1977 : groupe *tenuis;* THALER, 1994 : groupe *mansuetus*; THALER *et al.*, 1994 : groupe *annulatus*), la systématique du genre *Lepthyphantes* reste problématique.

En révisant les *Lepthyphantes* de France, nous avons trouvé deux espèces «oubliées» par SAARISTO & TANASEVITCH (*op. cit.*) qu'ils ne classèrent dans aucun de leurs groupes. La morphologie des organes sexuels secondaires de ces espèces est très différente de celle des autres groupes. Nous proposons la création d'un nouveau genre pour ces deux espèces.

Abréviations : MNHNP : Muséum national d'Histoire naturelle de Paris; MNCNM : Museo nacional de Ciencias naturales de Madrid.

DESCRIPTION

BORDEA n. gen.

Espèce-Type. — *Bordea cavicola* (Simon).

Étymologie. — Le genre est dédié à L. Borde en reconnaissance.

Diagnose

Linyphiidae de petite taille (1,8-2,5 mm). Couleur : céphalothorax, sternum, chélicères et pattes jaune orange; abdomen blanchâtre.

Céphalothorax sans protubérances; yeux normalement développés, presque équidistants. Chélicères pourvu de 3 denticules antérieurs et 5 postérieurs. Organe de stridulation composé de 20 stries peu évidentes.

Chétotaxie : fémur I pourvu d'une épine prolatérale, fémora II-IV mutiques; tibia muni de deux séries de 3 épines, chaque série composée d'une épine dorsale, une prolatérale et une rétrolatérale; métatarse pourvu d'une épine dorsale.

Pédipalpe (fig. 1-4, 9-11) : crin dorsal de la patella et du tibia faible, celui du tibia plus long, celui de la patella à peine plus long que le diamètre; tibia présentant au côté externe quelques denticules noirs; cymbium pourvu d'une courte saillie conique rétrolatérale; paracymbium pourvu dans sa concavité d'une carène ou d'une dent; apophyse supratégulaire se terminant en deux denticules; lamelle volumineuse, composée de deux branches inégales; embolus pointu, accompagné par un lobe latéral; tube séminifère pourvu d'une glande de Fickert composée de deux ampoules, l'une ovale, l'autre arrondie, puis se dirigeant tout droit vers l'embolus.

Épigyne (fig. 5-7, 12-14) pourvue d'un crochet très long ni plié ni aplati, non divisé en languette extérieure et languette intérieure comme chez *Lepthyphantes;* crochet beaucoup plus long que les plaques latérales; plaque médiane proéminente. Vulve (fig. 8, 15) : spermathèques ovales, canaux spermatiques se dirigeant d'abord vers le milieu de la base du crochet, puis tout droit vers son sommet, où se situe l'orifice de copulation.

Le genre est très voisin de *Lepthyphantes* et des autres genres cités ci-dessus classés auparavant dans *Lepthyphantes.* Il en diffère seulement par les organes sexuels secondaires. Les denticules du tibia du pédipalpe, la forme remarquable de la glande de Fickert, et le crochet de l'épigyne non plié ou aplati sont les caractères principaux qui distinguent ce nouveau genre de l'espèce-type de *Lepthyphantes.*

Bordea cavicola (Simon) n. comb.
(Fig. 1-8)

Porrhomma cavicola Simon, 1884 : 355 (descr. ♂, ♀).
Lepthyphantes cavicola Simon, 1929 : 736; Dresco, 1951 : 364.

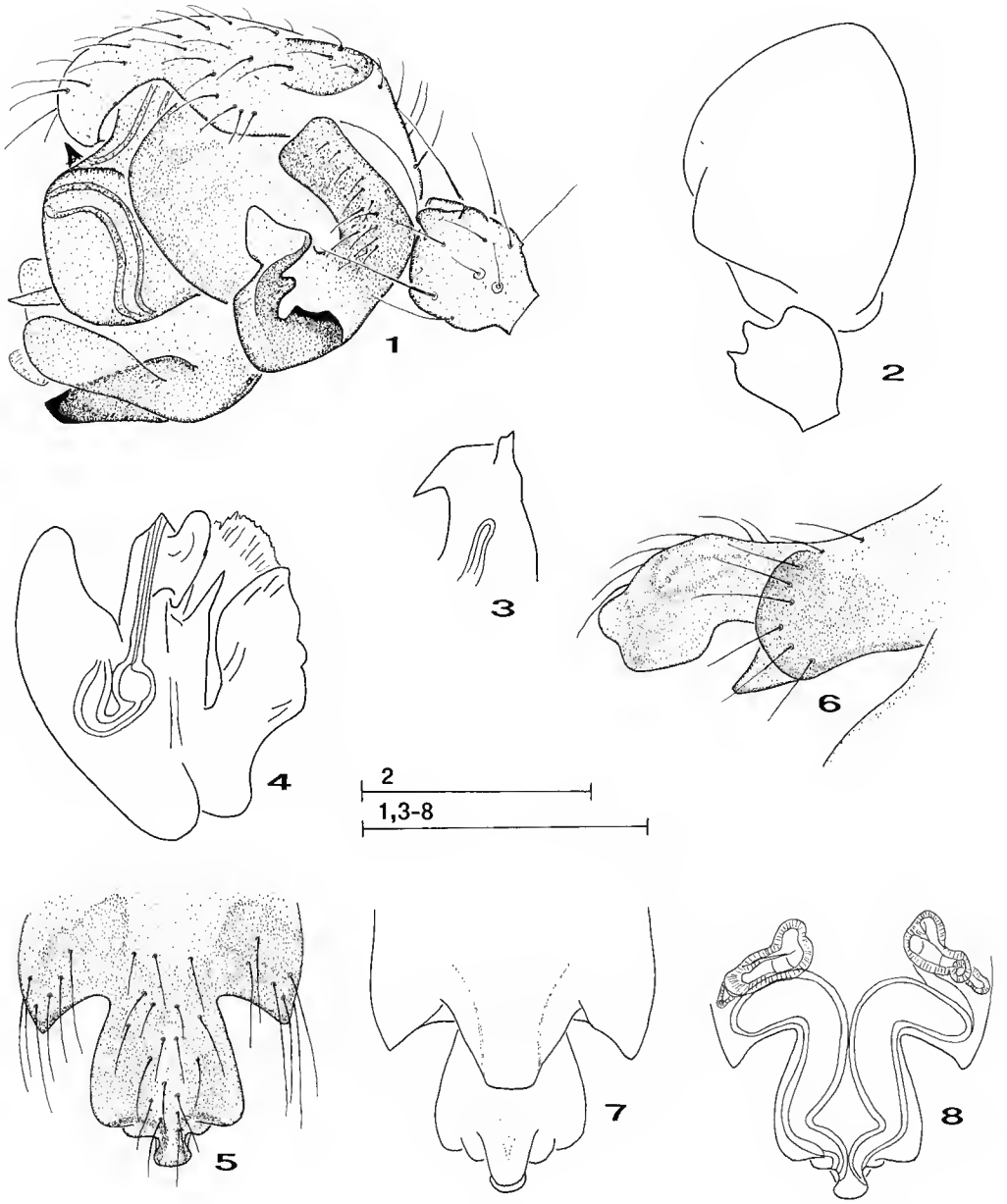

FIG. 1-8. — *Bordea cavicola* n. comb. 1, pédipalpe mâle, vue latérale ; 2, *idem*, vue dorsale ; 3, apophyse supratégulaire ; 4, division embolique ; 5, épigyne, vue ventrale ; 6, *idem*, vue latérale ; 7, *idem*, vue dorsale ; 8, vulve. Échelle : 0,25 mm.

Bordea cavicola *n. comb. 1, male palp, lateral view; 2,* idem, *dorsal view; 3, suprategular apophysis; 4, embolic division; 5, epigyne, ventral view; 6,* idem, *lateral view; 7,* idem, *dorsal view; 8, vulva. Scale: 0.25 mm.*

Lepthyphantes coiffaiti Denis, 1953 : 264 (descr. ♂). **n. syn.**

Matériel étudié et citations. — FRANCE : Basses-Pyrénées : Arudy, vallon de Molarode, holotype ♂ de *L. coiffaiti* (Denis, 1953 ; non examiné). Arudy, bois du Bager, paratype ♂ (Denis, 1953). Pyrénées-Orientales : col de Mentet, 1 600 m, 1 ♂ sous une pierre, 10 juin 1982, R. Bosmans leg. (collection R. Bosmans). – ESPAGNE : Navarra : Alsasua, Cueva de Orobe, lectotype ♀ de *Porrhomma cavicola*, par présente désignation. Paralectotypes : 1 ♀ appartenant à *L. cavicola*, 1 ♀ appartenant à *L. negrei* (MNHNP 4983).

Distribution. — Pyrénées espagnoles et françaises.

Diagnose

L'espèce est facilement reconnaissable par les grands denticules du tibia et la lamelle très allongée du pédipalpe chez le mâle, par le crochet aussi long que large de l'épigyne chez la femelle.

Discussion

Dans la description originale, Simon (1884), figure le pédipalpe du mâle et l'épigyne de la femelle. Pourtant, un mâle n'est pas présent dans la série type, comme déjà constaté par Dresco (1951). Selon lui, cette série type était composée de cinq femelles, mais nous n'en avons retrouvé que trois. Dresco écrit : « Une des femelles a un crochet différent des *cavicola* typiques... ». Il la prend pour une forme anormale, mais nous croyons qu'il s'agit ici d'un individu appartenant à *L. negrei*.

En 1953, Denis décrivit *L. coiffaiti*. Dans sa diagnose, il indique que l'espèce est très voisine de *L. negrei*, traitée ci-dessous, elle-même très proche de *L. cavicola*. Les types mâles de *L. cavicola* et de *L. coiffaiti* ne sont pas disponibles, mais d'après Simon (1884 : 356, fig. 128) et Denis (1953 : 265, fig. 3), et d'après un individu mâle capturé par nous-même, les deux espèces sont identiques, surtout en ce qui concerne la forme typique de la lamelle. Nous les considérons donc comme des synonymes.

Bordea negrei Dresco n. comb.
(Fig. 9-15)

Lepthyphantes negrei Dresco 1951 : 365 (descr. ♂, ♀) ; Denis, 1967 : 44, 47 ; Dresco & Hubert, 1968 : 493.

Lepthyphantes cavicola Machado 1940 : 9 (identification incorrecte).

Lepthyphantes ecclesiasticus Denis 1959 : 223 ; Dresco 1962 : 185. **n. syn.**

Lepthyphantes ictericus Simon 1929 : 599, 737 (descr. ♂, non ♀).

Matériel étudié et citations. — FRANCE : Ariège : gouffre de Peillot, 1 ♂, 1 ♀, 15 juillet 1945, série type de *L. negrei* (MNHNP) ; Montagagne, gouffre de Soulisquet, 1 ♀, 4 juin 1959 (MNHNP L398) ; étiquetté *L. ecclesiasticus*, mais cité par Denis (1967) comme *L. negrei*. Haute-Garonne : Montmaurin, grande grotte de la Seygouade (Denis, 1967). Hautes-Pyrénées : Bas-Nistos, grotte de l'Église, holotype femelle de *L. ecclesiasticus* (Denis, 1959) ; grotte de l'Ours (Dresco, 1951) ; grotte Soulabère (Dresco, 1951) ; grotte de la Pale, Saint-Pré-de-Bigorre, 1 ♀, octobre 1963 (Dresco & Hubert, 1968). — ESPAGNE : Navarra : Larraun, Cueva de Martinchurrito, 1 ♀, 22 août 1919 (sub. *L. cavicola*, MNCNM 53 ; Machado, 1940) ; Alsasua, Cueva de Orobe, 1 ♀ paralectotype de *L. cavicola* (MNHNP 4983).

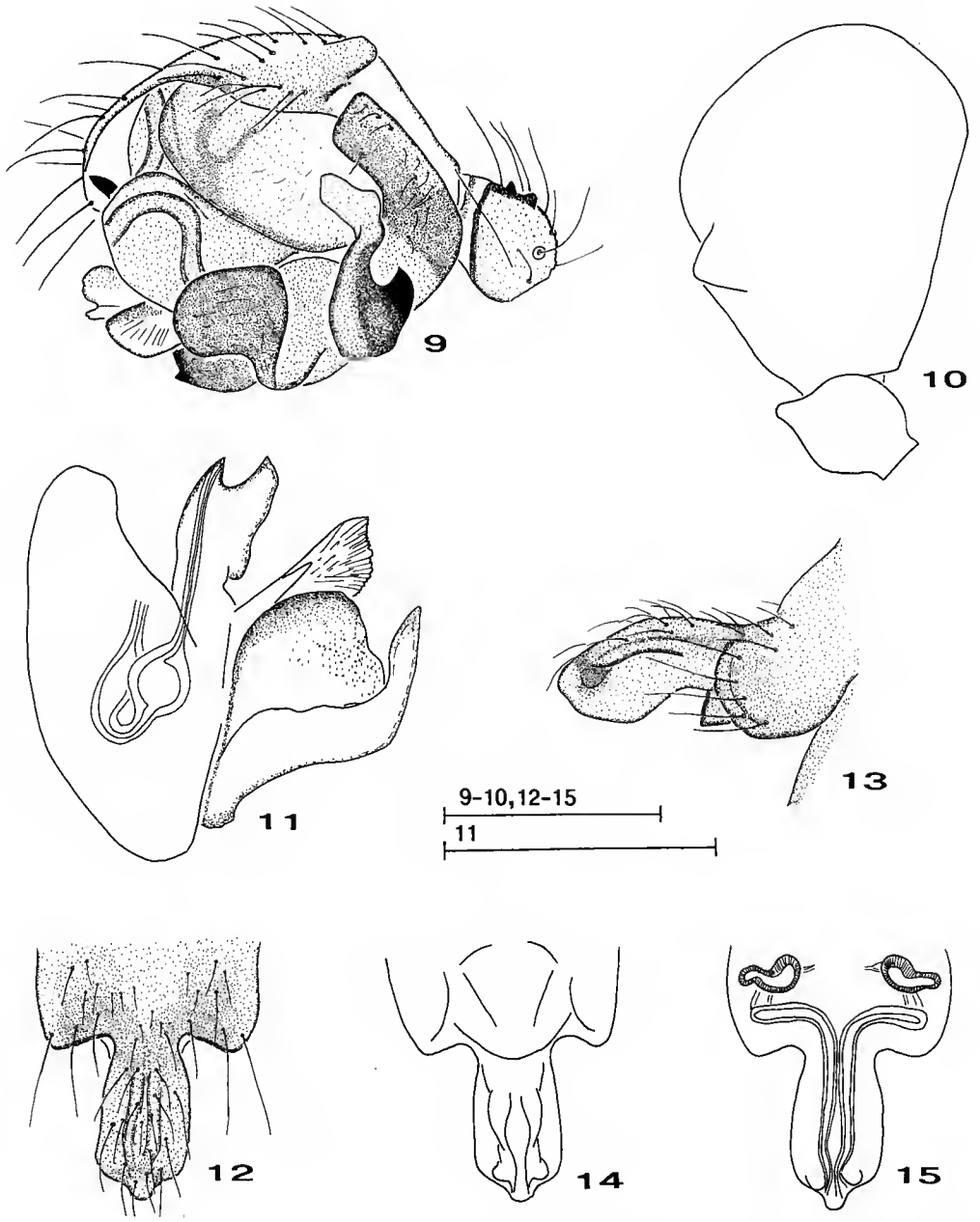

FIG 9-15. — *Bordea negrei* n. comb. 9, pédipalpe mâle, vue latérale ; 10, *idem*, vue dorsale ; 11, division embolique ; 12, épigyne, vue ventrale ; 13, *idem*, vue latérale ; 14, *idem*, vue dorsale ; 15, vulve. Échelle : 0,25 mm.

Bordea negrei *n. comb. 9, male palp, lateral view; 10,* idem, *dorsal view; 11, embolic division; 12, epigyne, ventral view; 13,* idem, *lateral view; 14,* idem, *dorsal view; 15, vulva. Scale: 0.25 mm.*

DIAGNOSE

Très voisine de *B. cavicola*. Les mâles diffèrent par les denticules du tibia moins prononcés, la dent de la branche distale du paracymbium non obtuse mais aiguë et la lamelle moins allongée ; les femelles par le crochet beaucoup plus long que large en vue ventrale et par la plaque ventrale moins proéminente.

DISCUSSION

Bordea negrei fut excellemment décrite et illustrée par DRESCO (1951) qui indique que l'espèce est voisine de *B. cavicola* et dont il donne également une figure de l'épigyne.

En 1959, DENIS décrit des Pyrénées une femelle qu'il nomme *Lepthyphantes ecclesiasticus*. Déjà DRESCO (1962) douta de la validité de cette espèce, se demandant s'il ne s'agissait pas d'un synonyme de *L. negrei*. En effet, les figures de DRESCO (1951) de l'épigyne de *L. negrei* et de DENIS (1959) de l'épigyne de *L. ecclesiasticus* sont presque identiques. On a d'ailleurs retrouvé au MNHNP un individu identifié par DENIS portant une étiquette «*L. ecclesiasticus*», mais cité par lui en 1967 comme *L. negrei*. Il est probable que DENIS ait constaté la synonymie, mais sans jamais la publier lui-même.

Un autre cas intéressant et énigmatique est celui d'un mâle et de deux femelles, décrits comme *Lepthyphantes ictericus* par SIMON (1929) de la grotte de l'Ours dans les Hautes-Pyrénées. SIMON figura l'épigyne de la femelle ressemblant beaucoup à un *Centromerus*. L'examen de cette femelle a confirmé ce point de vue. Le mâle fut perdu accidentellement (SIMON, 1929 : 599, en note). Son pédipalpe n'a pas été représenté mais dans la clé, les deux espèces sont distinguées :

— Tibia, vu de profil, élevé en cône vertical, pourvu, sur sa pente antérieure (assez loin de l'angle), d'un petit denticule noir obtus ; crin dressé subapical ; paracymbium noir, pourvu dans sa concavité, vers le milieu, d'une petite apophyse comprimée tronquée ; tarse gros, offrant au bord externe (avant l'échrancure normale) une courte saillie conique ..... *L. ictericus*

— Tibia, vu de profil, légèrement convexe, armé, à l'angle apical, d'un petit denticule fauve, conique, dirigé en avant, et, un peu plus en arrière, de quelques petites granulations noires piligères. Paracymbium très fortement courbé en demi-cercle, mutique au bord interne de sa concavité, sa branche antérieure chitinisée rouge passant au noir à l'extrémité. Lanière du bulbe vue de profil d'abord dirigée en avant puis coudée presque verticalement, enfin coudée en avant en forme de Z ..... *L. cavicola*

Nous pensons que cette description de *L. cavicola* correspond à celle de *L. negrei*, autre habitant de la grotte de l'Ours (DRESCO, 1951). Le mâle et la femelle de *L. ictericus* ne sont donc pas conspécifiques. La femelle appartient à une espèce voisine des *Centromerus*, et le mâle est celui de *B. negrei*.

Le mâle retrouvé au MNCNM sous le nom *Lepthyphantes cavicola* et cité sous ce nom par MACHADO (1940) concerne également *Bordea negrei*.

Dans la série type, ont été retrouvés dans le même tube des individus de *Bordea cavicola* et de *B. negrei*, provenant de la Cueva de Orobe, la seule localité citée par SIMON. Les deux

espèces vivraient donc ensemble dans la même grotte. Ceci reste pourtant à confirmer, car SIMON avait l'habitude de mélanger des récoltes de différentes localités. Il se peut que des spécimens de *B. negrei* capturés par BOLIVAR en 1919 et cités beaucoup plus tard par MACHADO (1940) comme *B. cavicola*, aient été envoyés par BOLIVAR à SIMON qui les aurait incorporés dans sa collection.

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Nous remercions vivement C. ROLLARD et J. HEURTAULT (MNHNP) et A. G. VALDECASAS (MNCNM) pour le prêt de spécimens.

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Description de trois nouveaux genres et quatre nouvelles espèces de scorpions Buthidae de Madagascar

par Wilson R. LOURENÇO

Résumé. — Trois nouveaux genres, *Pseudouroplectes*, *Microcharmus* et *Neogrosphus*, et quatre nouvelles espèces, *Pseudouroplectes betschi*, *Microcharmus cloudsleythompsoni*, *Tityobuthus guillaumeti* et *Tityobuthus pococki* appartenant à la famille des Buthidae sont décrits de Madagascar. La découverte des trois nouveaux genres représente une intéressante contribution pour la clarification des origines et des affinités de la faune malgache.

Mots-clés. — Scorpion, Madagascar, Buthidae, nouveaux genres.

Description of three new genera and four new species of Buthidae Scorpions from Madagascar

Abstract. — Three new genera, *Pseudouroplectes*, *Microcharmus* and *Neogrosphus* and four new species, *Pseudouroplectes bestchi*, *Microcharmus cloudsleythompsoni*, *Tityobuthus guillaumeti* and *Tityobuthus pococki* belonging to the Buthidae family are described from Madagascar. These three new genera represent an interesting contribution to our understanding of the origins and affinities of the fauna of Madagascar.

Keywords. — Scorpion, Madagascar, Buthidae, new genera.

W. R. LOURENÇO, *travail réalisé au Laboratoire de Zoologie (Arthropodes) du Muséum national d'Histoire naturelle, 61, rue Buffon, F-75005 Paris.*

INTRODUCTION

Dans le cadre d'une étude biogéographique sur les scorpions de Madagascar, j'ai été amené à examiner les collections des scorpions provenant de Madagascar et déposées au Muséum national d'Histoire naturelle, Paris.

Une grande partie des collections de Paris ont déjà servi à la description de nouveaux genres et de nouvelles espèces notamment par GERVAIS (1844), SIMON (1880) et KRAEPELIN (1901).

À la suite de la révision monographique de FAGE (1929) et de la revue des Arachnides de MILLOT (1948), la faune scorpionique de Madagascar semble assez bien étudiée et peu de nouveaux taxa ont été ajoutés. Quelques compléments sont apportés par VACHON (1969, 1979).

La découverte de trois nouveaux genres, dont deux peuvent être classés parmi les micro-Scorpions, augmente significativement le taux de taxa endémiques de la grande île, mais apporte surtout des éléments nouveaux, très précieux, sur les affinités de la faune scorpionique malgache.

Dans le présent travail, je me limiterai à décrire les nouveaux taxa avec quelques commentaires sur leurs probables positions phylogénétiques. L'ensemble du problème biogéographique

sera traité dans l'étude mentionnée ci-dessus qui sera présentée lors du Colloque international de biogéographie de Madagascar qui se tiendra à Paris en septembre 1995.

DESCRIPTION

Genre **PSEUDOUROPLECTES** n. g.
(Fig. 1, 4-8)

DIAGNOSE

Scorpions de petite taille; longueur totale des adultes d'environ 22-25 mm. Coloration générale jaunâtre avec quelques taches rougeâtres esquissées sur le mésosoma; anneau V du métasoma et telson d'une couleur davantage rougeâtre clair. La morphologie générale rappelle celle du genre *Uroplectes* Peters, 1861. Granulation faiblement marquée. Carènes des pédipalpes discrètes; corps lisse avec une carène médiane; anneaux du métasoma avec des carènes bien marquées; les dorsales avec un granule postérieur spiniforme. Anneaux I et II avec 10 carènes; III et IV à 8 carènes; V avec 5 carènes; les ventrales plus discrètes. Peignes sans fulcres; absence

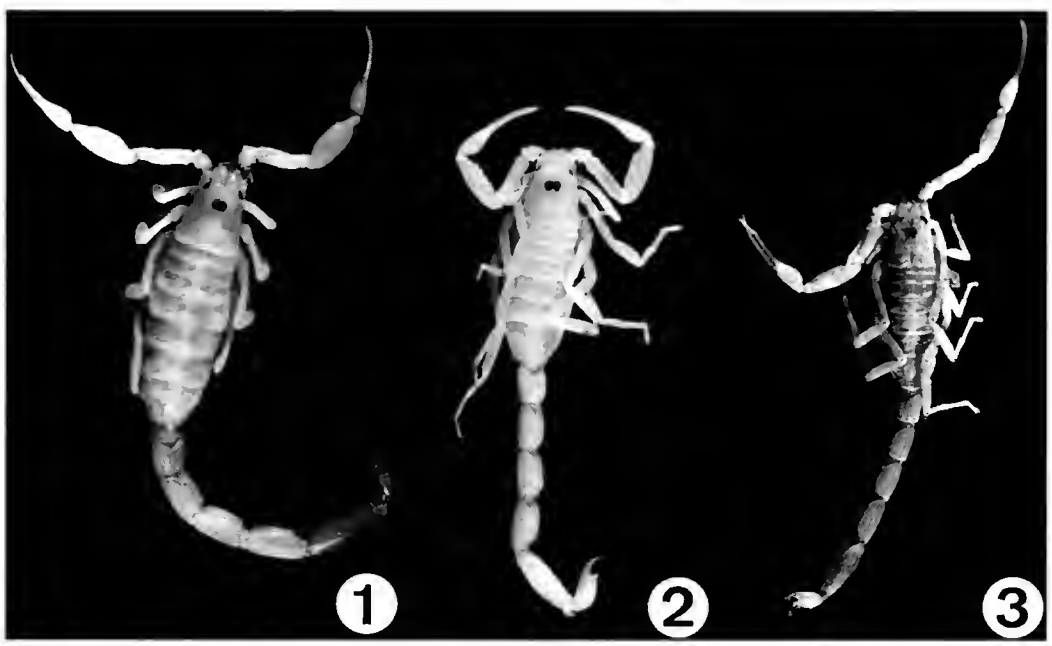

FIG. 1-3. — Exemplaires holotypes en vue dorsale. 1, *Pseudouroplectes betschi* (femelle); 2, *Tityobuthus guillaumeti* (mâle); 3, *Tityobuthus pococki* (mâle).

Dorsal view of holotypes. 1, Pseudouroplectes betschi *(female); 2,* Tityobuthus guillaumeti *(male); 3,* Tityobuthus pococki *(male).*

d'une dent interne plus développée. Deux éperons basitarsaux à la quatrième patte. Chélicères avec la dentition caractéristique des Buthidae (VACHON, 1963); les deux dents basales sont très discrètes, difficiles à individualiser. Tranchant des doigts mobiles des mains des pédipalpes avec 7 séries de granules. Trichobothriotaxie du type A avec la disposition α pour les trichobothries de la face dorsale du fémur des pédipalpes (VACHON, 1963, 1965).

Le nouveau genre *Pseudouroplectes* rappelle le genre africain *Uroplectes*. Il peut cependant être facilement distingué d'*Uroplectes* par l'absence de fulcra aux peignes, l'absence de la dent interne plus développée et la présence d'un sternum à mi-chemin entre la forme subtriangulaire et subpentagonale.

Pseudouroplectes betschi n. sp.
(Fig. 1, 4-8)

MATÉRIEL-TYPE. — Holotype femelle : plateau Mahafaly, province de Tuléar, Madagascar, 28 juillet 1967 (J.-M. BESTCH) (90 m alt., zone à dolines, près de l'Andramanoetse Be; haut fourré arbustif à Euphorbes et Didiéréacées; chasse à vue, sous bois mort et pierres). Déposé au Muséum national d'Histoire naturelle, Paris, MNHN RS-8512.

ÉTYMOLOGIE. — Le nom spécifique est attribué en hommage au Pr Jean-Marie BETSCH du Laboratoire d'Écologie du Muséum national d'Histoire naturelle, Paris.

DESCRIPTION

Coloration générale jaunâtre avec présence de taches rougeâtres longitudinales esquissées sur le mésosoma. Anneau V du métasoma et telson rougeâtre clair. Face ventrale des prosoma et mésosoma jaunâtre pâle. Le tubercule oculaire et les yeux latéraux sont noirs.

Morphologie

Prosoma : plaque prosomienne avec le bord antérieur concave. Tubercule oculaire antérieur par rapport au centre de la plaque prosomienne; yeux médians séparés par un diamètre oculaire. Trois paires d'yeux latéraux. Carènes du prosoma et du mésosoma très discrètes; seule une carène médiane est bien perceptible sur le mésosoma. Plaque prosomienne et tergites du mésosoma dépourvus de granulation, pratiquement lisses.

Métasoma : tous les anneaux avec des carènes bien marquées; les dorsales avec un granule postérieur spiniforme; anneaux I et II avec 10 carènes; III et IV à 8 carènes; anneau V arrondi avec 5 carènes; les ventrales sont plus discrètes que chez les autres anneaux. Vésicule lisse fortement allongée. Aiguillon dépourvu d'épine ventrale. Sternites à stigmates linéaires aplatis. Peignes avec 19-18 dents (paratype avec 16-15); absence de fulcres et d'une dent interne plus développée. Deux éperons basitarsaux à la quatrième patte.

Pédipalpes lisses avec des carènes pratiquement imperceptibles. Tranchant des doigts mobiles de la main avec 7 séries longitudinales de granules fins, disposés en ligne droite légèrement oblique. Chélicères avec la dentition caractéristique des Buthidae. Les deux dents basales sont peu individualisées et semblent être fusionnées en une seule. Trichobothriotaxie du type A-α, orthobothriotaxique (VACHON, 1973, 1975). Un paratype femelle avec les mêmes données que pour l'holotype.

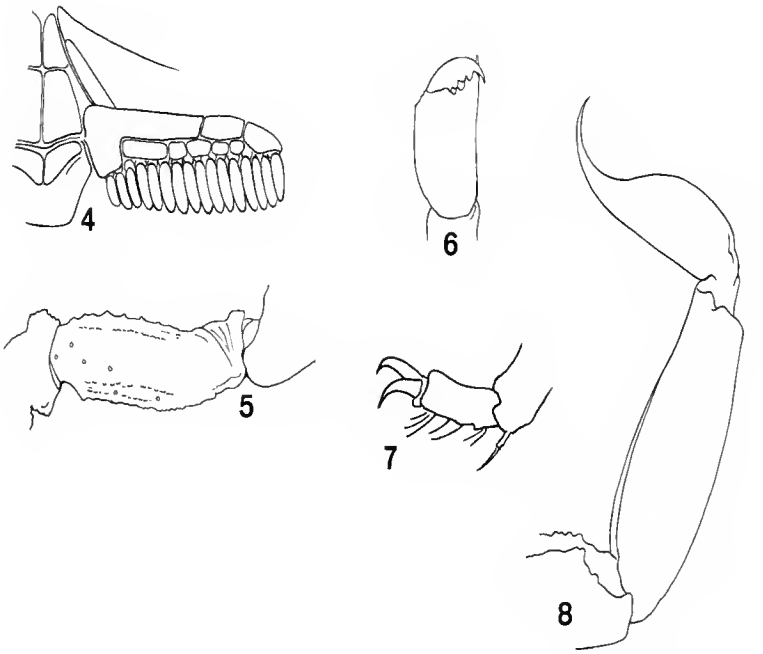

FIG. 4-8. — *Pseudouroplectes betschi*, paratype femelle. 4, peigne, opercule-génital et sternum ; 5, fémur, vue dorsale ; 6, chélicère ; 7, tarse ; 8, anneau V du métasoma et telson.

Pseudouroplectes betschi, *female paratype. 4, pectines, genital operculum and sternum; 5, femur, dorsal view; 6, chelicerae; 7, tarsus; 8, segment V of metasoma and telson.*

Mensurations (en mm) de l'exemplaire décrit : plaque prosomienne, longueur 2,6 ; largeur antérieure 1,5 ; largeur postérieure 2,5. Anneau caudal I, longueur 1,4 ; largeur 1,3. Anneau caudal V, longueur 3,3 ; largeur 1,1 ; hauteur 1,1. Telson, largeur 0,7 ; hauteur 0,7. Pédipalpes : fémur, longueur 2,1 ; tibia, longueur 2,7 ; pince, longueur 3,6 ; doigt mobile, longueur 2,7.

Genre **MICROCHARMUS** n. g.
(Fig. 9-11)

DIAGNOSE

Scorpion de petite taille : longueur totale des adultes d'environ 20 mm. Coloration générale jaunâtre ; seuls les yeux sont de couleur noire. La morphologie générale rappelle celle du genre *Charmus* Karsch, 1879 et, pour certains caractères, tels la forme des peignes et celle du sternum, le nouveau genre paraît se rapprocher de *Microtityus* K. W., 1966. Cependant, dans ce deuxième cas, il ne peut s'agir que d'une convergence. Granulation générale peu marquée, faible ou

moyenne selon les régions du corps. Carènes des pédipalpes et du corps très faiblement marquées ; celles des anneaux du métasoma bien marquées sur les quatre premiers anneaux ; les dorsales avec un granule distal spiniforme ; carènes ventrales peu marquées. Peignes très petits, sans fulcres ; un éperon basitarsal à la quatrième patte. Chélicères avec la dentition caractéristique des Buthidae (VACHON, 1963) ; les deux dents basales sont très petites, peu marquées et difficiles à distinguer. Tranchant des doigts mobiles des mains des pédipalpes avec 6 (7) séries de granulations légèrement obliques. Trichobothriotaxie du type A avec la disposition α pour les trichobothries de la face dorsale du fémur des pédipalpes (VACHON, 1973, 1975).

Le nouveau genre *Microcharmus* rappelle le genre *Charmus*, connu uniquement de l'Inde et du Sri Lanka, par la morphologie de son sternum nettement subpentagonale et par la disposition des trichobothries de la face dorsale du fémur des pédipalpes. Le nouveau genre peut néanmoins être distingué du genre *Charmus*, par l'absence de fulcres et un nombre très réduit de dents aux peignes (10-10).

Microcharmus cloudsleythompsoni n. sp.
(Fig. 9-11)

MATÉRIEL-TYPE. — Holotype femelle : Zangoa, Nord Ouest, Madagascar, 1947 (J. MILLOT). Déposé au Muséum national d'Histoire naturelle, Paris, MNHN RS-4811.

ÉTYMOLOGIE. — Le nom spécifique est attribué en hommage au Pr John L. CLOUDSLEY-THOMPSON, University of London.

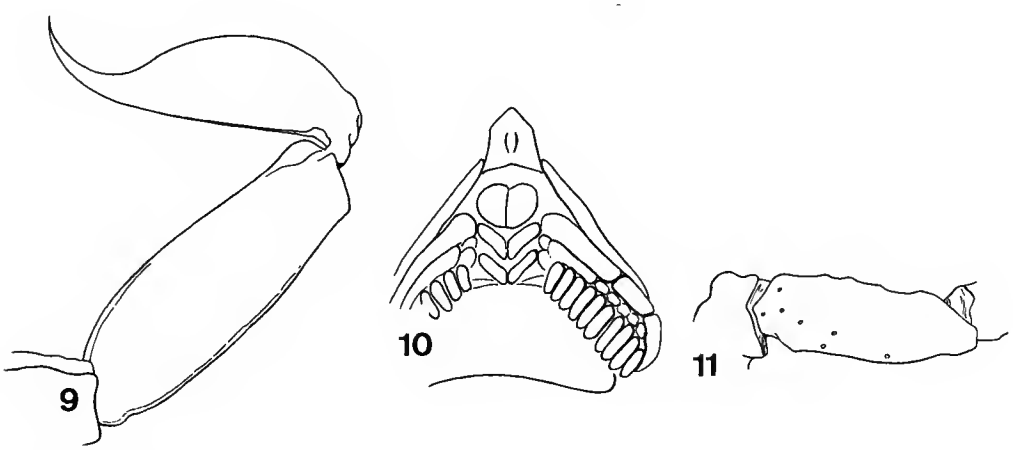

FIG. 9-11. — *Microcharmus cloudsleythompsoni*, holotype mâle. 9, anneau V du métasoma et telson ; 10, peignes, opercule-génital et stemum ; 11, fémur, vue dorsale.

Microcharmus cloudsleythompsoni, *male holotype. 9, segment V of metasoma and telson; 10, pectines, genital operculum and sternum; 11, femur, dorsal view.*

DESCRIPTION

Coloration générale uniformement jaunâtre. Face ventrale des prosoma et mésosoma jaunâtre pâle. Le tubercule oculaire et les yeux latéraux sont noirs.

Morphologie

Prosoma : plaque prosomienne avec le bord antérieur légèrement concave. Tubercule oculaire antérieur par rapport au centre de la plaque prosomienne ; yeux médians séparés par un diamètre oculaire environ. Trois paires d'yeux latéraux. Carènes du prosoma et du mésosoma très faiblement marquées. Granulation de la plaque prosomienne et des tergites du mésosoma moyennement à faiblement marquée.

Métasoma : carènes bien marquées sur les quatre premiers anneaux ; les dorsales avec un petit granule distal spiniforme ; les ventrales plus discrètement marquées ; anneau V arrondi avec des carènes moins marquées que chez les quatre autres anneaux. Anneaux I et II avec 10 carènes ; III et IV à 8 carènes ; anneau V avec 5 carènes. Vésicule lisse très allongée. Aiguillon dépourvu d'épine ventrale. Sternites à stigmates linéaires aplatis. Peignes très petits avec un nombre de dents particulièrement faible, 10-10, quasiment atypique chez un Buthidae, mais plutôt caractéristique des quelques micro-Scorpions ; absence de fulcres. Sternum subpentagonal, caractéristique de certains Buthidae tels *Charmus* et *Microtityus*.

Pédipalpes très lisses ; carènes très faiblement marquées. Tranchant des doigts mobiles des mains des pédipalpes avec 7 (6) séries de granulations légèrement obliques. Chélicères avec la dentition caractéristique des Buthidae ; les deux dents basales sont néanmoins très petites, peu marquées et difficiles à distinguer et semblent être fusionnées en une seule (VACHON, 1963). Trichobothriotaxie du type A-α, orthobothriotaxique. Pas de paratypes.

Mensurations (en mm) de l'exemplaire décrit : plaque prosomienne, longueur 1,6 ; largeur antérieure 1,1 ; largeur postérieure 1,8. Anneau caudal I, longueur 0,9 ; largeur 1,0. Anneau caudal V, longueur 1,9 ; largeur 0,8 ; hauteur 0,7. Telson, largeur 0,5 ; hauteur 0,6. Pédipalpes : fémur, longueur 1,3 ; tibia, longueur 1,7 ; pince, longueur 2,5 ; doigt mobile, longueur 1,7.

Genre **NEOGROSPHUS** n. g.
(Fig. 12)

Lors de la description de *Grosphus griveaudi* Vachon (VACHON, 1969), celui-ci soulève plusieurs remarques sur le classement de cette espèce dans le genre *Grosphus* Simon. Ainsi, VACHON (1969) affirme : « La détermination des spécimens qui ont permis la création de cette espèce nouvelle nous a posé maints problèmes. Car *G. griveaudi* possède des caractères qui l'isolent nettement des six autres espèces connues de *Grosphus* ». Il affirme plus loin : « Il est donc fort possible que l'espèce *griveaudi* appartienne à un sous-genre nouveau ou à un genre nouveau. »

Au cours de la présente étude, après examen de la totalité de la série typique, constituée de nombreux spécimens, j'en arrive à la conclusion que cette espèce doit être placée dans un genre différent, pour lequel une nouvelle diagnose est donnée ci-dessous.

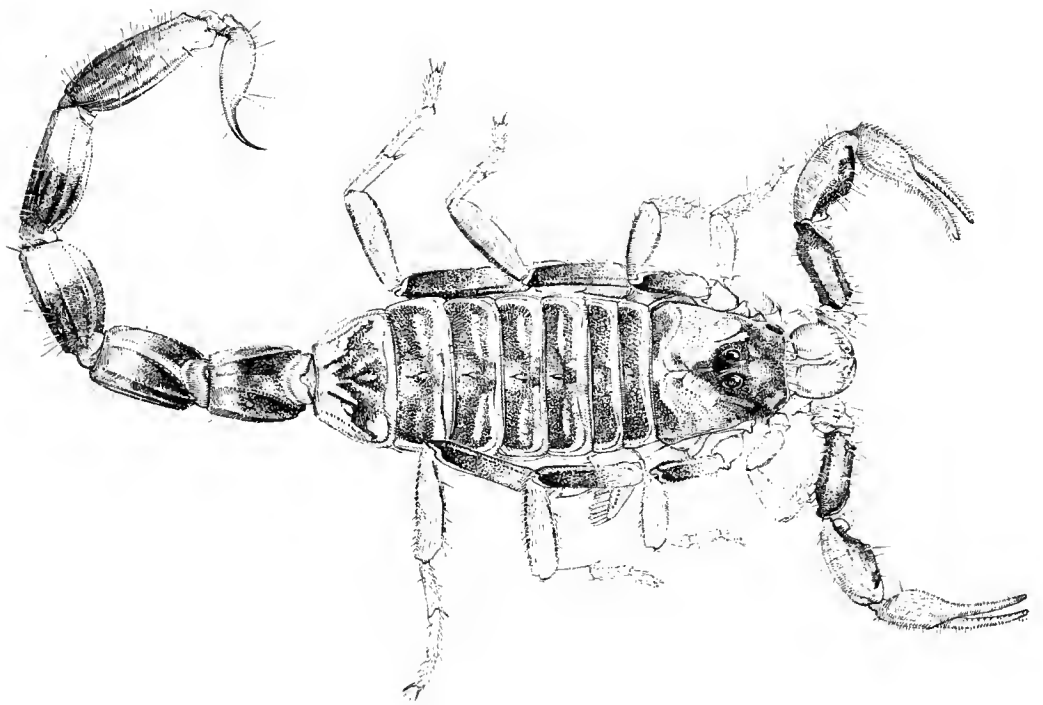

FIG. 12. — Vue dorsale d'ensemble de la femelle type de *Neogrosphus griveaudi* (Vachon), espèce-type du genre (d'après VACHON, 1969).

Dorsal view of the female type of Neogrosphus griveaudi *(Vachon), type species of the genus (from VACHON, 1969).*

DIAGNOSE

Scorpions de taille petite et moyenne ; les mâles ont environ la moitié de la taille des femelles (24 mm contre 45 mm pour les femelles). Le nouveau genre se particularise aussi par un nombre de séries de granulations au tranchant des doigts mobiles des pinces des pédipalpes (8-9) bien inférieur à ceux retrouvés sur les espèces de *Grosphus* (de 11 à 14). Puis, ainsi que le souligne VACHON (1969), une caractéristique encore plus importante est la possession, sous la dent terminant le doigt mobile, de trois granules externes alors que tous les autres *Grosphus* en ont quatre. Par ailleurs, la dent terminale est très développée et pointue chez *Neogrosphus*. Enfin, la position de la trichobothrie V_2 de la face ventrale de la main est particulièrement ventrale, caractéristique déjà observée pour le genre *Parabuthus* (VACHON, 1969), tandis que la languette tarsale est très réduite comparée à celle observée chez les espèces de *Grosphus*.

Le travail de VACHON (1969) illustre déjà fort bien ces différents points. La totalité du matériel que j'ai pu étudier est répertoriée dans ce même travail.

Tityobuthus guillaumeti n. sp.
(Fig. 2, 13-17)

MATÉRIEL-TYPE. — Holotype mâle : Iaraka, baie d'Antongil, Madagascar, 17 novembre 1969 (J.-M. BESTCH) (700 m alt., forêt dense humide de moyenne altitude). Déposé au Muséum national d'Histoire naturelle, Paris, MNHN RS-7268.

ÉTYMOLOGIE. — Le nom spécifique est attribué en hommage au Dr Jean-Louis GUILLAUMET de l'ORSTOM, Paris.

DESCRIPTION

Coloration générale uniformement jaunâtre. Face ventrale du prosoma et du mésosoma jaunâtre pâle. Le tubercule oculaire et les yeux latéraux sont noirs.

Morphologie

Prosoma : plaque prosomienne avec le bord antérieur légèrement concave. Tubercule oculaire antérieur par rapport au centre de la plaque prosomienne ; yeux médians séparés par trois quarts d'un diamètre oculaire. Trois paires d'yeux latéraux. Carènes du prosoma et du mésosoma pratiquement imperceptibles. Granulation du corps en général très faible ou inexistante.

Métasoma : tous les anneaux avec des carènes faiblement marquées ou absentes. Carènes ventrales de l'anneau V dentillées. Vésicule lisse très allongée. Aiguillon avec une épine ventrale

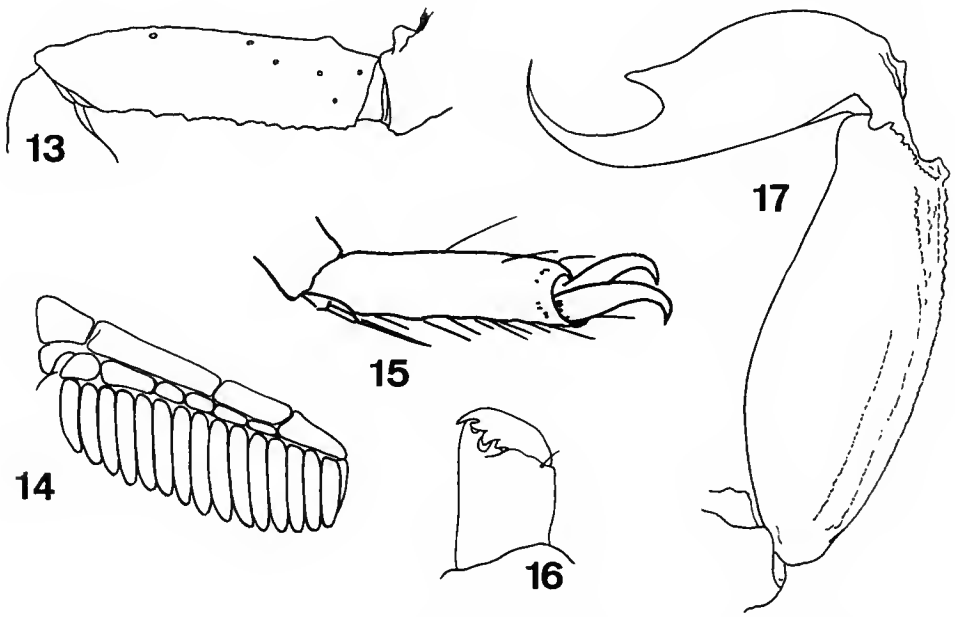

FIG. 13-17. — *Tityobuthus guillaumeti*, holotype mâle. 13, fémur, vue dorsale ; 14, peigne ; 15, tarse ; 16, chélicère ; 17, anneau V du métasoma et telson.

Tityobuthus guillaumeti, *male holotype. 13, femur, dorsal view; 14, pectine; 15, tarsus; 16, chelicerae; 17, segment V of metasoma and telson.*

bien développée. Sternites à stigmates plutôt linéaires aplatis. Peignes très grands avec 15-14 dents, absence de fulcres. Deux éperons basitarsaux à la quatrième patte.

Pédipalpes très lisses. Seules trois dents sont remarquées sur la face interne du tibia. Tranchant des doigts mobiles de la main avec 7 séries longitudinales de granules très fins disposés presque en ligne droite, l'une derrière l'autre. Chélicères avec la dentition caractéristique des Buthidae, cependant les deux dents basales se distinguent très peu l'une de l'autre et semblent quasiment fusionnées en une seule (VACHON, 1963). Trichobothriotaxie du type A-α, orthobothriotaxique (VACHON, 1973, 1975). Pas de paratypes.

Mensurations (en mm) de l'exemplaire décrit : plaque prosomienne, longueur 2,1 ; largeur antérieure 1,4 ; largeur postérieure 2,1. Anneau caudal I, longueur 1,1 ; largeur 1,2. Anneau caudal V, longueur 2,7 ; largeur 1,0 ; hauteur 1,1. Telson, largeur 0,8 ; hauteur 0,8. Pédipalpe : fémur, longueur 2,2 ; tibia, longueur 2,3 ; pince, longueur 3,5 ; doigt mobile, longueur 2,1.

Cette nouvelle espèce est voisine de *Tityobuthus baroni* (Pocock), par sa taille et sa morphologie générale. Cependant elle peut être distinguée de *T. baroni* par l'absence de fulcres aux peignes. L'étude d'une cinquantaine d'exemplaires de *T. baroni* de la collection du Muséum a démontré que les fulcres sont toujours présentes, y compris dans tous les exemplaires immatures. VACHON *(in litt.)* m'avait suggéré que cette espèce pourrait être placée dans un genre nouveau, cependant il me semble plus prudent de retarder une telle décision.

Tityobuthus pococki n. sp.
(Fig. 3, 18-22)

MATÉRIEL-TYPE. — Holotype mâle : W. Bekopaka Antsingy, Madagascar, juillet 1970 (P. GRIVEAUD). Déposé au Muséum national d'Histoire naturelle, Paris MNHN RS-5418.

ÉTYMOLOGIE. — Le nom spécifique est attribué en hommage à R. I. POCOCK, créateur du genre *Tityobuthus*.

DESCRIPTION

Coloration générale globalement jaunâtre, avec la présence de quelques taches brunâtres sur la plaque prosomienne. Le tubercule oculaire et les yeux latéraux sont noirs. Deux taches longitudinales brunâtres sur le mesosoma. Ensemble de la face ventrale et sternites jaunâtres. Métasoma : trois premiers anneaux jaunâtres ; IV et V rougeâtres. Vésicule rougeâtre.

Morphologie

Prosoma : plaque prosomienne avec le bord antérieur légèrement concave. Tubercule oculaire antérieur par rapport au centre de la plaque prosomienne ; yeux médians séparés par moins d'un diamètre oculaire. Trois paires d'yeux latéraux. Carènes du prosoma et du mesosoma discrètes ; seule une carène est bien perceptible sur les tergites I à VI du mesosoma. VII avec 5 carènes. Plaque prosomienne et tergites du mesosoma avec une granulation moyenne.

Métasoma : tous les anneaux avec des carènes bien marquées ; les dorsales avec un granule postérieur spiniforme ; anneaux I et II avec 10 carènes ; III avec 8 carènes ; anneaux IV et V avec des carènes très discrètes ; les carènes ventrales sont absentes sur tous les anneaux ; anneau V très arrondi. Vésicule lisse, allongée. Aiguillon très long avec une épine ventrale aiguë. Ster-

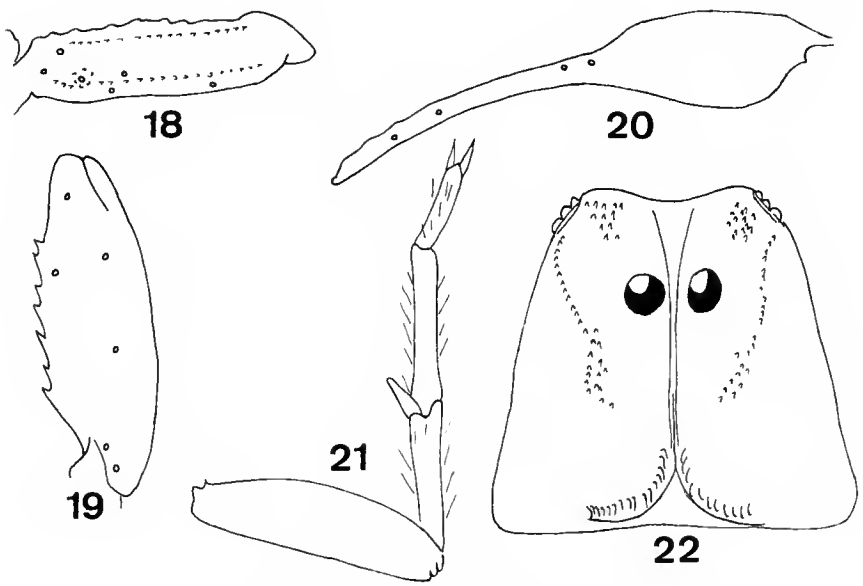

FIG. 18-22. — *Tityobuthus pococki*, holotype mâle. 18, fémur, vue dorsale ; 19, tibia, vue dorsale ; 20, pince, vue latérale ; 21, section de la quatrième patte avec éperon tibial ; 22, plaque prosomienne.

Tityobuthus pococki, *male holotype. 18, femur, dorsal view; 19, tibia, dorsal view; 20, chelae, lateral view; 21, section of fourth leg with tibial spur; 22, carapace.*

nites à stigmates linéaires aplatis. Peignes avec 22-23 dents. Epéron tibial très développé, ce qui différencie cette espèce des autres du genre (VACHON, 1979).

Pédipalpes avec des carènes moyennement marquées. Fémur avec 5 carènes ; tibia à carènes peu définies et à face interne avec des granules spiniformes ; pince plutôt lisse. Tranchant des doigts mobiles de la main avec 8 séries longitudinales de granules fins, disposés en ligne droite légèrement oblique ; présence de granules accessoires plus gros. Chélicères avec la dentition caractéristique des Buthidae. Les deux dents basales sont peu individualisées. Trichobothriotaxie du type A-α, orthobothriotaxique (VACHON, 1973, 1975). Pas de paratypes.

Mensurations (en mm) de l'exemplaire décrit : plaque prosomienne, longueur 2,9 ; largeur antérieure 2,1 ; largeur postérieure 3,0. Anneau caudal I, longueur 2,0 ; largeur 1,7. Anneau caudal V, longueur 3,5 ; largeur 1,5 ; hauteur 1,5. Telson, largeur 0,9 ; hauteur 1,0. Pédipalpes : fémur, longueur 2,8 ; tibia, longueur, 3,7 ; pince, longueur 6,0 ; doigt mobile, longueur 4,1.

Cette nouvelle espèce se situe, par sa taille, dans une position intermédiaire entre les trois espèces connues du genre *Tityobuthus* ; elle est plus grande que *Tityobuthus baroni* (Pocock) et plus petite que *Tityobuthus gracilis* (Fage). Elle peut être facilement distinguée des espèces citées par la présence d'éperons tibiaux bien développés, très discrets ou absents chez les autres espèces (VACHON, 1979). Enfin, elle se distingue de *Tityobuthus guillaumeti* par la présence de fulcres aux peignes.

CONSIDÉRATIONS PRÉLIMINAIRES SUR LA PHYLOGÉNIE DES NOUVEAUX TAXA DÉCRITS

Dans une optique tout à fait préliminaire, il me semble nécessaire de souligner l'importance de la découverte de trois nouveaux genres à Madagascar pour la clarification des origines et affinités de la faune scorpionique actuelle.

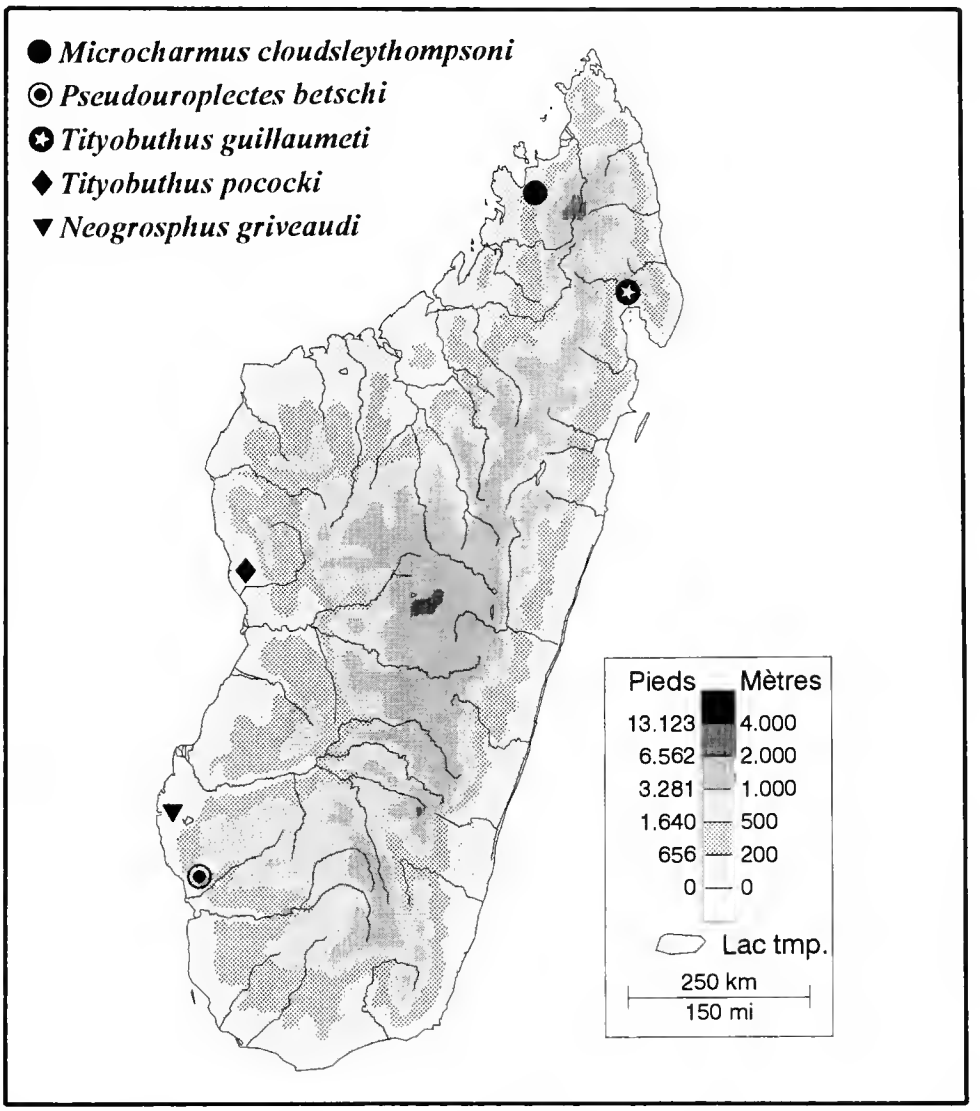

FIG. 23. — Carte avec l'indication des stations typiques des genres et des espèces nouvelles décrites dans le présent travail.
Map with indication of the typical localities of the new genera and new species.

La position de *Pseudouroplectes* semble être relativement simple à préciser car ses affinités avec le genre africain *Uroplectes* peuvent être facilement admises. Le genre *Uroplectes* est largement réparti dans la région afrotropicale, à l'exception du Zaïre et d'une partie de l'Afrique occidentale recouvrant le Cameroun et le Gabon (LAMORAL, 1979).

La découverte du nouveau genre *Microcharmus* est particulièrement intéressante, car ses affinités avec le genre *Charmus* démontrent la possible existence d'un lien entre la faune scorpionique malgache et celle de la région indo-malaise ; le genre *Charmus* n'était jusqu'à présent connu que de l'Inde et du Sri Lanka.

Le genre *Neogrosphus* est sans aucun doute associé à *Grosphus*, et sa différenciation a certainement eu lieu plus récemment que celle d'autres genres malgaches. La création des trois genres nouveaux, associée à la description de quatre espèces nouvelles augmente d'une manière significative la diversité de la faune scorpionique de la grande île et son taux d'endémicité.

Ces quelques conclusions préliminaires seront discutées dans un article actuellement en cours de rédaction sur la biogéographie de Madagascar. Dans cet article global, seront clarifiées les questions des origines, affinités et différenciation de la faune malgache actuelle.

Remerciements

Je suis très reconnaissant à la direction du Laboratoire de Zoologie, Arthropodes, du Muséum national d'Histoire naturelle, Paris, de m'avoir facilité l'étude du matériel utilisé dans le présent travail. Mes remerciements vont aussi tout particulièrement à M. J. REBIÈRE pour sa contribution à la réalisation de plusieurs dessins illustrant le présent travail.

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Cyst morphology of European branchiopods (Crustacea: Anostraca, Notostraca, Spinicaudata, Laevicaudata)

by Alain THIÉRY, Ján BRTEK and Charles GASC

Abstract. — A comparative analysis of cyst (= resting egg) size and shell architecture by scanning electron microscopy is reported in 40 species of "large branchiopods", belonging to 21 genera from all the families inhabiting inland waters of Europe. This paper follows one on the geographic distribution of the European branchiopods where 72 species and subspecies belonging to 22 genera and 13 families were listed (BRTEK & THIÉRY, 1995). Particular attention has been paid to cyst shape and morphology of the external shell surface. The results are discussed in the light of existing literature. When the taxonomic value of the external shell surface pattern shows its limits, the combination size/surface pattern seems more useful, being sometimes species-specific, while in other cases (such as in *Branchipus*, *Tanymastix*, *Cyzicus*, *Imnadia*) it appears to reflect taxonomic relationships of higher rank. In other cases, a third character, the structure of the cyst envelope, observable in fractured cysts, must be taken into account to separate cysts (as in *Artemia* sp. and *Branchinectella*). "Large branchiopods" eggs can provide new taxonomic information that is useful in the definition of natural groups.

Keywords. — Cyst morphology, resting egg, Europe, Crustacea, Anostraca, Notostraca, Spinicaudata, Laevicaudata, scanning electron microscopy, taxonomy.

Morphologie des œufs de branchiopodes européens (Crustacea: Anostraca, Notostraca, Spinicaudata, Laevicaudata)

Résumé. — La morphologie des œufs (= œufs de résistance) de 40 espèces de branchiopodes (Anostraca, Notostraca, Spinicaudata, Laevicaudata) appartenant à 21 genres représentant toutes les familles peuplant les eaux stagnantes continentales d'Europe, est décrite au moyen du microscope électronique à balayage. Cette étude fait suite à l'article de BRTEK & THIÉRY (1995) qui dresse l'inventaire actuel de ces crustacés branchiopodes en Europe et illustre la distribution géographique des 72 espèces et sous-espèces répertoriées, représentantes de 22 genres et 13 familles. La forme des œufs et la morphologie externe de leur enveloppe sont décrites, les résultats étant confrontés aux données bibliographiques. Dans de nombreux cas, les ornementations de surface sont des critères fiables permettant une identification spécifique ou générique. Lorsque ces ornementations ne présentent pas de caractéristiques suffisantes pour établir une discrimination des œufs, il est alors nécessaire de considérer la combinaison diamètre/ornementations de surface qui peut être spécifique ou parfois générique comme c'est le cas pour les genres *Branchipus*, *Tanymastix*, *Cyzicus* et *Imnadia*. Dans quelques cas, un troisième caractère, la structure interne de l'enveloppe de l'œuf, observable en coupe, doit être considéré pour séparer des œufs d'aspect identique mais d'espèces différentes (cas pour *Artemia* sp. et *Branchinectella media*). La morphologie des œufs de branchiopodes, ayant une incontestable valeur taxonomique, devrait être prise en compte pour compléter les études sur la phylogénie de ces crustacés.

Mots-clés. — Morphologie, œufs de résistance, Europe, Crustacea, Anostraca, Notostraca, Spinicaudata, Laevicaudata, microscope électronique à balayage, taxonomie.

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INTRODUCTION

"Large branchiopods" – fairy shrimps (Anostraca), tadpole shrimps (Notostraca) and clam shrimps (Spinicaudata + Laevicaudata) – are crustaceans living in inland temporary freshwaters, or sometimes saltwaters. As they live in physically and chemically fluctuating astatic habitats, with recurrent phases of complete drying (temporary ponds, ditches, salterns...), these crustaceans present adaptations to desiccation, the main one being the production of only one sort of egg – thick-walled resting eggs (= cysts). The morphology of cysts has been described since the work of DADAY (1910 to 1927) and in several cases specific distinctness has been hypothetized. During the mid- and late 1980s, the micromorphology of cysts has been a central topic in "large branchiopods" biology. Scanning electron microscopy has been used to obtain accurate images of fine surface structures and increasing knowledge has led a number of authors to consider and discuss the taxonomic importance of the micromorphology and size of the cysts (review *in* THIÉRY & GASC, 1991; De WALSCHE *et al.*, 1991; MURA, 1992a, b). While for several countries cyst morphology has been studied, (Spain: ALONSO & ALCARAZ, 1984, all the orders; Italy: MURA, 1986, 1992a, both only anostracans; France: THIÉRY & GASC, 1991, all the orders), no global view on the European scale is available. The present study is the first one to attempt a synthesis.

MATERIAL AND METHODS

IDENTIFICATION

Species identifications were made using adult morphology (second antenna and penes of the male; female ovisac), using DADAY (1910 to 1927), LINDER (1941), BRTEK (1959, 1964, 1966), LONGHURST (1955), STRASKRABA (1965a, b; 1966). Branchiopod taxonomy follows FRYER (1987) and BRTEK & THIÉRY (1995).

The surveyed area is shown in Fig. 1.

SEM STUDIES

Cysts were removed from female ovisacs, kept in 10% formaldehyde, then fixed in a bath of KAAD (30% kerosene, 60% absolute ethanol, 5% acetic acid, 5% dioxane) for 24 h (see THIÉRY & GASC, 1991). From preserved females, we chose only individuals with well formed complete egg-shells. The egg-shell pattern changes from fertilization to time of deposition (see THIÉRY, 1985 for *Triops*; MURA, 1992b for *Chirocephalus diaphanus*). After CO_2 critical point drying, cysts were coated with gold and then observed using a Cambridge Stereoscan 360 at an acceleration voltage of 20 KV and a working distance varying from 9-10 mm for the smaller cysts (clam shrimps) to 25 mm for the bigger ones (*Branchinecta* and tadpole shrimps). Some technical data are given on Fig. 4c.

MEASUREMENTS

Cyst diameter and surface ornamentation (spines, ridges...) were measured with a SEM numerical point-point system (see example in Figs 4b – crosses, and 4d – vertical lines) and

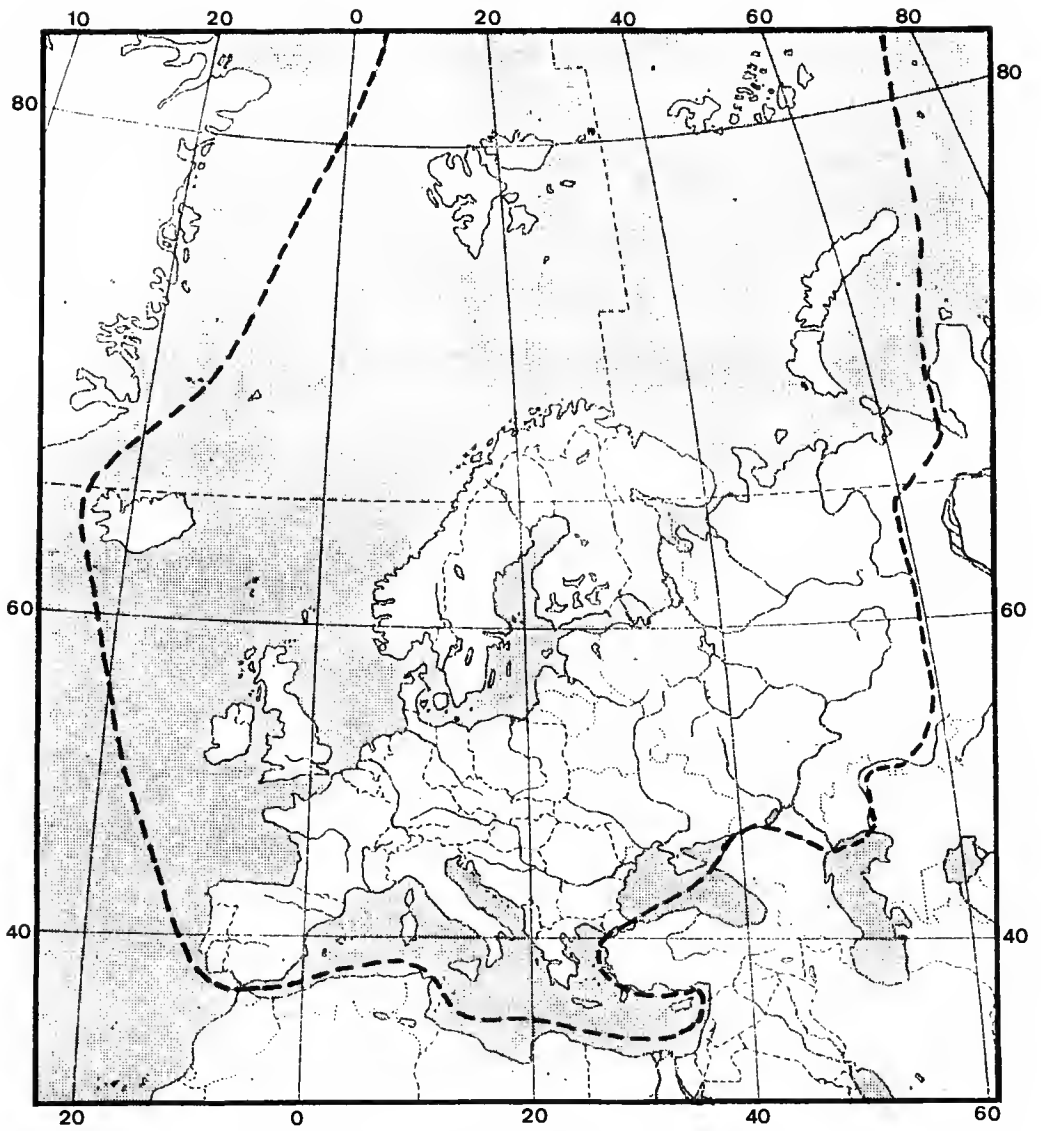

FIG. 1. — Area surveyed in the study of cyst morphology of "large branchiopods".
Aire géographique prise en compte pour l'étude de la morphologie des œufs des « grands Branchiopodes ».

sometimes on calibrated SEM photonegatives. Diameters cited from the literature were measured from published calibrated photographs. To study the variability of cyst diameter we use a Variation Index (V. I.) defined as: maximum diameter-minimum diameter/mean diameter, in per cent.

MATERIAL EXAMINED

ANOSTRACA

Artemia parthenogenetica Bowen & Sterling, 1978: saltworks of Salin-de-Giraud, Camargue, S. France, 6. 5. 1989, coll. A. THIÉRY (Figs 7h, 8a).

Artemia tunisiana Bowen & Sterling, 1978 (= bisexual strain): coastal saltworks, Sète-Villeroy, S. France, 5. 5. 1989, coll. A. THIÉRY (Fig. 8b).

Branchinecta ferox (Milne-Edwards, 1840): Hurbanovo, 17. 4. 1956, and Palarikovo, 22. 4. 1969, SW Slovakia, both in coll. J. BRTEK (136) (Figs 4b, c).

Branchinecta minuta Smirnov, 1948: Dnepropetrovsk-district, Ukraine, 6. 4. 1937, coll. S. SMIRNOV (Figs 4f, g; 5b-d).

Branchinecta orientalis Sars, 1901: Illmitz, Lake Kirchsee, Austria, 26. 5. 1963, coll. J. VORNATSCHER (Fig. 4e).

Branchinecta paludosa (Müller, 1788): High Tatra mountains, Horne Furkotske Lake, N. Slovakia. (Figs 4a; 5a).

Branchinecta tolli (Sars, 1897): Laptevis Sea, Stolbovoj Island, Russia, 29. 2. 1985, and Tiksi, Yakutia, Russia, 1. 8. 1985, coll. N. VEKHOFF (Figs 4d; 5e-g).

Branchinectella media (Schmankevitch, 1873): Troick District, Kudaj-Sugur lake, Kazachstan, 11. 4. 1932, coll. S. SMIRNOV (Figs 7e; 8e).

Branchinella spinosa (Milne-Edwards, 1840): salterns of Salin-de-Giraud, Camargue, Southern France, 6. 5. 1989 (Fig. 8c).

Branchipus blanchardi Daday, 1908: High Alps, type locality on the Cristol Plateau, France, 24. 8. 1988, coll. A. THIÉRY (Fig. 6j, k).

Branchipus schäefferi Fischer, 1834: Tekovské Luzany (Sec. Kertész 1956 as "Nagysallo", SW Slovakia, 27. 5. 1972, coll. J. BRTEK (1513) syn. *visnyai* (Fig. 6h), and Rivesaltes, 19. 11. 1987, and Plain of Crau, 26. 3. 1994, S. France, coll. A. THIÉRY (Fig. 6i).

*Branchipus laevicornis** Daday, 1910: Eregli, Asia Minor, coll. E. DADAY, 1912 MNHN Bp273 (Fig. 7d).

*Chirocephalus bairdi** (Brauer, 1877): Berekhat Hitin, Israel, 24. 3. 1983, coll. R. ORTAL (Fig. 10a-c).

Chirocephalus chyzeri (Daday, 1890): Maly Hores, 24. 4. 1970, and Vel'ky Kamenec, SE Slovakia, 24. 4. 1970, coll. J. BRTEK (745, 752) (Fig. 9c, d).

Chirocephalus carnuntanus (Brauer, 1877): Gbelce, 28. 4. 1966, and Hurbanovo, 14. 4. 1967, SW Slovakia, coll. J. BRTEK (228) (Figs 9i; 10i-l).

Chirocephalus diaphanus Prévost, 1803: Saint-Maximin, S. France (Provence), 7. 2. 1988, coll. A. THIÉRY (Fig. 8j).

Chirocephalus diaphanus carinatus (Daday, 1910): Musala, Bulgaria, alt. 2300 m, 8. 8. 1962, coll. J. GULICKA (Fig. 9b).

Chirocephalus josephinae (Grube, 1853): Ust'-Kut, Asian Russia, 4. 6. 1925, coll. S. SMIRNOV (Figs 9h; 10h).

Chirocephalus orghidani Brtek, 1966: Planitza, Romania, 18. 4. 1960, coll. P. BANARESCU (Figs 8i; 10e).

Chirocephalus pelagonicus Petkovski, 1986: Golemo Konjari, Macedonia, 4. 5. 1985, coll. S. PETKOVSKI (Fig. 9a).

Chirocephalus salinus (Daday, 1910): "Trepadoules" Porto Vecchio, SE Corsica, 28. 1. 1988, coll. A. THIÉRY (Figs 8k; 10d).

Chirocephalus shadini (Smirnov, 1928): Bol'-Zatin, 25. 4. 1970, and Zatin, 15. 4. 1969, SE Slovakia, coll. J. BRTEK (755, 399) (Figs 9g; 10f).

Chirocephalus slovacicus Brtek, 1971: Jesenské, 12. 4. 1968, Janice, 22. 4. 1970, and Lenartovce-Vlkyna, 21. 4. 1981, S. Slovakia, coll. J. BRTEK (365, 718, 1873) (Figs 9e; 10g).

Chirocephalus spinicaudatus Simon, 1886: France, MNHN Bp157, coll. E. SIMON (25. 96), E. DAOAY det. 1909 (Fig. 9f).

Drepanosurus birostratus (Fischer, 1851): Tomsk, Russia, 25. 4. 1919 (Fig. 8h: immature cyst).

Drepanosurus hankoi (Dudich, 1927): Kralovsky Chlmec, SE Slovakia, 15. 4. 1969, coll. J. BRTEK (398) (Figs 6a, b; 7a).

Linderiella massaliensis Thiéry & Champeau, 1988: Saint-Maximin, S. France, 7. 2. 1988, coll. A. THIÉRY (Figs 7f; 8d).

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* Species living outside the study area, but described for comparison.

Polyarteuia forcipata Fischer, 1851: Murmansk, Russia, 1898 (No 228) (Fig. 7b).

Siphonophanes grubii (Dybowski, 1860): Moravia, coll. J. Hhrabé 27. 4. 1958, MNHN Bp 161, and Slovakia mer-occid. Sv. Jur. 25. 4. 1958 J. Brtek leg., MNHN Bp 260 (Figs 6f, g; 7c).

Streptocephalus torvicoruis (Waga, 1842): Malé Trakany, 19. 7. 1969, and Dobra, 19. 7. 1969, SE Slovakia, coll. J. Brtek (545, 552) (Fig. 6c-e).

Tanymastix stagnalis (Linnaeus, 1758): Fontainebleau forest, France, 9. 8. 1988, coll. A. Thiéry (Fig. 8f).

Tanymastix stellae Cottarelli, 1968: "Trepadoules" South of Porto Vecchio, Corsica, 28. 1. 1988, coll. A. Thiéry (Fig. 8g).

NOTOSTRACA

Lepidurus apus (Linnaeus, 1758): Kamenicnà, SW Slovakia, 14. 5. 1970, coll. J. Brtek (840); Gavoti, 21. 2. 1988, and Rochefort du Gard, S. France, both in coll. A. Thiéry (Figs 11e; 12a, d, f-h).

Lepidurus arcticus (Pallas, 1793): Sachanika west Coast of Novaya Zemlya, Russia, 12. 9. 1925, coll. Zool. Inst. AN USSR (Fig. 12b, e).

Lepidurus couesii Packard, 1875: Ulan Bator, Mongolia, 7. 7. 1970, coll. Z. Peregi (Fig. 12c).

Triops cancriformis (Bosc, 1801): Komàrovce, SE Slovakia, 17. 7. 1969, coll. J. Brtek; Opoul, 26. 3. 1988, and Plain of Crau, 26. 3. 1994, S. France, coll. A. Thiéry (Fig. 11a-d).

SPINICAUDATA

Limnadia lenticularis (Linnaeus, 1761): Komarno, 26. 7. 1969, and Kava, 30. 5. 1973, SW Slovakia, coll. J. Brtek (602) (Fig. 13a-c).

Imnadia yeyetta Hertzog, 1935: Sulany, 15. 5. 1970, and Medvedov, 16. 5. 1970, SW Slovakia, coll. J. Brtek (893) (Fig. 13d, e), and La Galère, Plain of Crau, S. France, 26. 3. 1994, coll. A. Thiéry.

Cyzicus tetracerus (Krynicki, 1830): Dobra, 3. 6. 1970, and Jenkovce, 31. 5. 1970, SE Slovakia, coll. J. Brtek (984, 1065); Gavoti, Provence, S. France, 21. 2. 1988, coll. A. Thiéry (Fig. 13f, g, i).

Eocyzicus orieutalis Daday, 1913: Astrahan, Russia, 3. 6. 1968. (Fig. 13h, j).

Leptestheria dahalaceucis (Rüppel, 1837): Sul'any, 15. 5. 1970, and Nové Zàmky, 29. 5. 1973, SW Slovakia, coll. J. Brtek (866, 1779) (Fig. 14a-e).

Eoleptestheria ticiuensis (Balsamo-Crivelli, 1859): Novosad-Jastrabie, 1. 6. 1970, and Zemplìnske Jastrabie-Oborìn, 1. 6. 1970, SE Slovakia, coll. J. Brtek (1005, 1009) (Fig. 14f).

LAEVICAUDATA

Lynceus brachyurus Müller, 1776: Kralovsky Chlmec, 3. 6. 1970, SE Slovakia, coll. J. Brtek (1043) (Fig. 14g, h).

RESULTS

Size-Diameter

Results are presented in Table I and Fig. 2. In Table I, the species are listed in taxonomic order; in Fig. 2 by increasing size. For each species, our original data (labelled "this study") have been supplemented by data from the literature. In all cases, except where diameters are related to erroneous scale bars, as in Alonso & Alcaraz (1984) for *Branchinecta ferox* and *B. cervantesi* or in Mura (1992, Pl. 2, p. 237) for six species of *Chirocephalus*, the cysts are of more or less consistent diameter. In most cases, our results agree with data in the literature.

In most cases, the Variation Index (VI) ranges from 3 to 30%. However, in several species, such as in *Branchipus schäefferi*, *Tanymastix stagnalis*, *Streptocephalus torvicornis*, *Chirocephalus diaphanus*, and *Artemia*, the index is higher, from 30 to 55%. The lesser values of the Variation Index, indicating a relative constancy in cyst diameter whatever the geographical origin of the population, are found in species with restricted areas of distribution, while values of V. I.

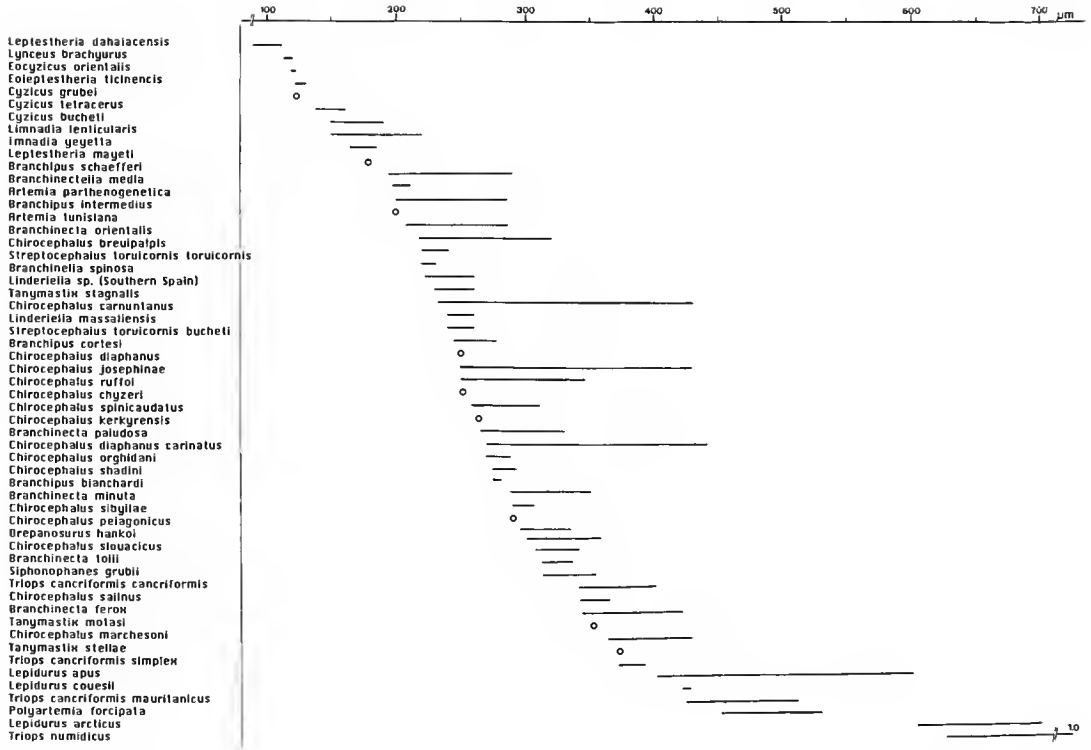

FIG. 2. — Diameters in µm (low and high values from this paper and from available literature) of the cysts of European branchiopods ranged from the smaller to the larger. Open circles indicate single measurements.

Diamètres en µm (valeurs inférieures et supérieures d'après les résultats de cette étude et les données bibliographiques) des œufs des Branchiopodes d'Europe classés par ordre croissant de taille. Les cercles indiquent des mesures isolées.

are greater in common and widely distributed species (for geographical distribution in Europe, see BRTEK & THIÉRY, 1995).

The V. I. might be also linked with the diversity of measurements (number of authors or precision of the measuremts, as shown in Fig. 3 which illustrates the correlation between the Variation Index and the number of citations in the literature: V. I. (%) = 5.558 number of citations + 0.39 ($n = 31$, $r^2 = 0.633$, $P < 0.05$).

The smallest cysts are those of spinicaudatans and laevicaudatans, ranging from 95 to 209 µm. Those of anostracans range from 198 to 527 µm and of notostracans from 350 to 780 µm. The Arctic species *Polyartemia forcipata* and *Lepidurus arcticus* have the largest cysts of the European "large branchiopods".

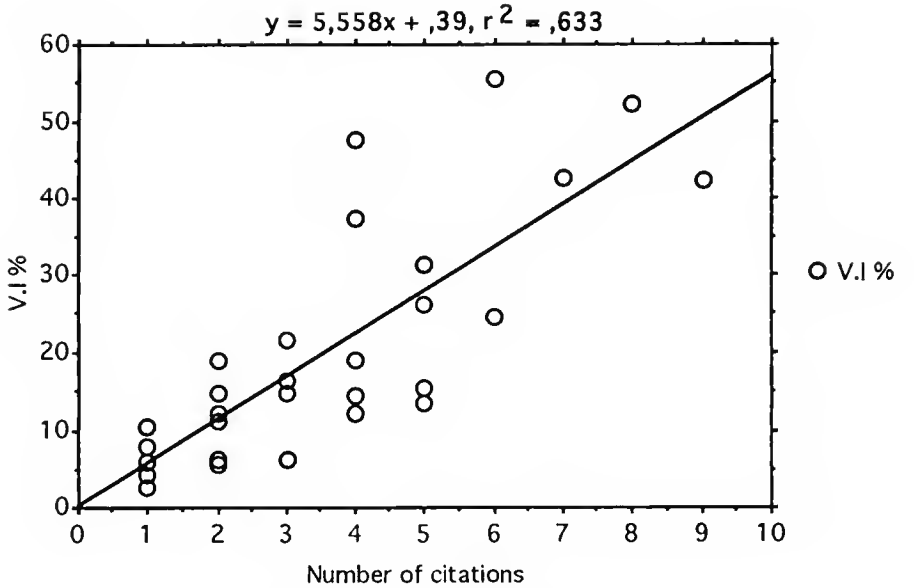

FIG. 3. — Relation between variation index (%) and number of citations in the literature. V. I. % = 5.558 citations + 0.39 (n = 31, r^2 = 0.633, P < 0.05).

Relation entre l'indice de variation (en %) et le nombre de références dans la littérature. V. I. (%) = 5,558 citations + 0,39 (n = 31, r^2 = 0,633, P < 0,05).

CYST MORPHOLOGY

ANOSTRACA (Table I and Figs 4 to 14): except for the cysts of the genus *Tanymastix* which are lenticular, all those of anostracans are more or less spherical. Their surface may be smooth, as in *Artemia* and *Branchinectella media*, or, more usually ornamented by ridges, spines, depressions or crests.

Polyartemiidae (Fig. 7b): *Polyartemia forcipata* has a large spherical cyst, with a rugose surface, with rounded spines shorter than 10 µm in length, as described by MURA (1992b, Plate 5.3).

Branchinectidae (Figs 4, 5): except for those of *Branchinecta tolli* which are slightly rugose (Figs 4d; 5e, f, g), the cysts of the European species of *Branchinecta* are characterized by low ridges which delineate large polygons (Figs 4a-c, e-g; 5a, b). (GILCHRIST, 1978; MURA & THIÉRY, 1986; MURA, 1991a, and MAEDA-MARTINEZ *et al.*, 1992, 1993). The cysts of *Branchinecta paludosa* and *B. ferox* are similar in appearance and of the same size, but the polygonal areas tend to be larger in the former. Likewise the cysts of *Branchinecta orientalis* and *B. minuta* are very similar (Fig. 4e, f, g). They are smaller than those of *B. paludosa* and *B. ferox*, and their ridges are more rounded and delineate smaller polygonal areas. No objective character distinguishes them. Concerning the internal structure of the egg-shell, its spongy aspect in *Branchinecta*

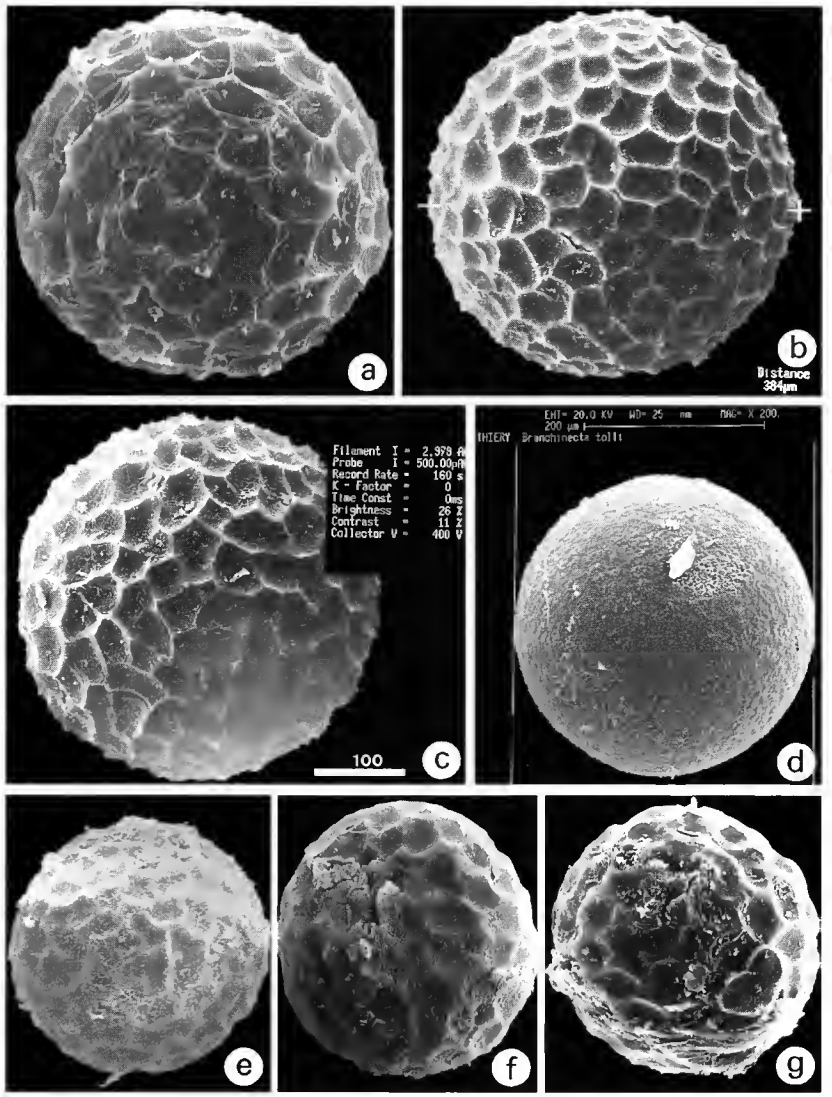

FIG. 4. — Cysts of anostraca: a) *Branchinecta paludosa*; b), c) *B. ferox*; d) *B. tolli*; e) *B. orientalis*; f), g) *B. minuta*. (common scale bar in µm).

Œufs d'Anostraca : a) Branchinecta paludosa ; *b), c)* B. ferox ; *d)* B. tolli ; *e)* B. orientalis ; *f), g)* B. minuta *(échelle commune en µm).*

minuta (Fig. 5c, d), agrees with the findings of GILCHRIST (1978) for *B. ferox*. In *B. tolli,* the cyst wall is thin with thick low roots (Fig. 5f). No data are available for *B. orientalis*.

Artemiidae (Figs 7, 8): cysts of *Artemia* are spherical and smooth (Figs 7h; 8a, b), as described in many studies (MAZZINI, 1978; GILCHRIST, 1978; MURA & THIÉRY, 1986; SPOTTE &

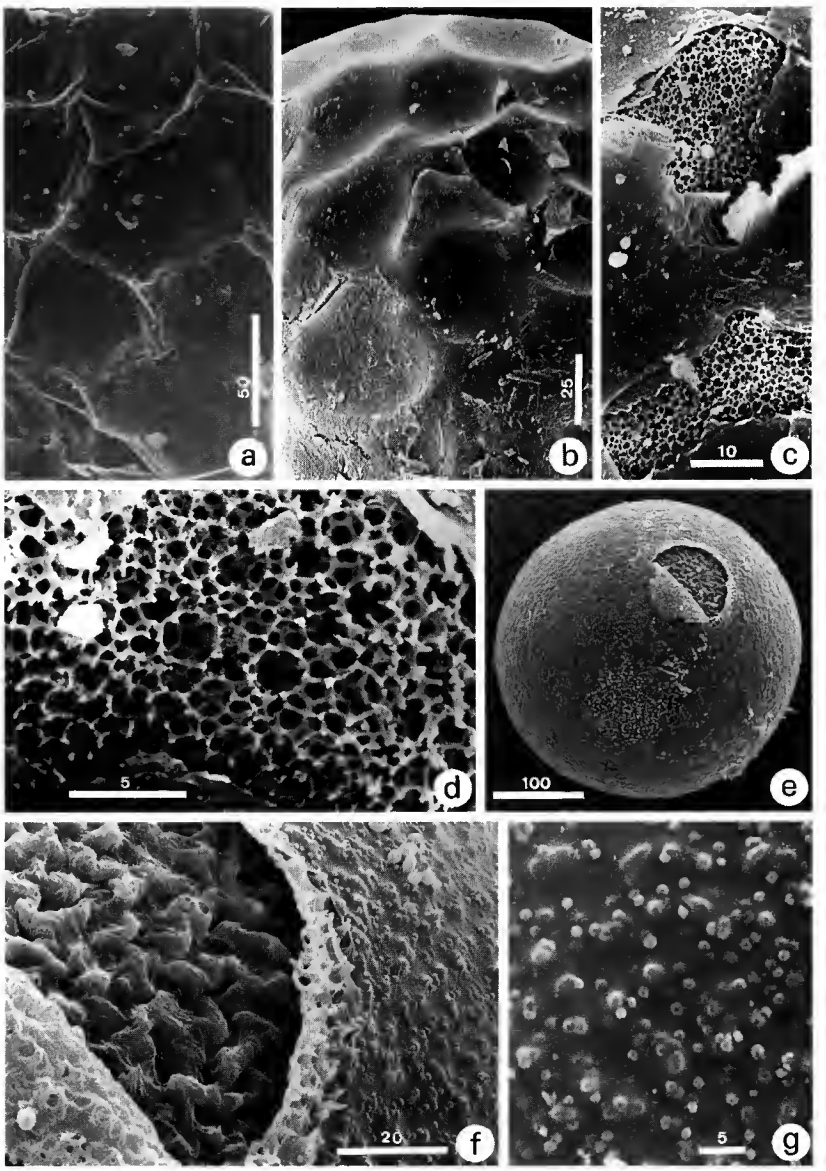

FIG. 5. — Cysts of Anostraca: a) details of *Branchinecta paludosa*, b) *idem*, *B. minuta*, c) *idem*, outer membrane cracked showing spongy structure; d) detail of spongy structure; e) *Branchinecta tolli*, f) *Branchinecta tolli*, detail of a cracked part of egg shell; g) *B. tolli*, detail of surface showing little rounded pits. (scale bars in µm).

Œufs d'Anostraca : a) détail, Branchinecta paludosa ; *b)* idem, B. minuta ; *c)* B. minuta, *la membrane externe déchirée permet de voir la structure spongieuse ; d)* B. minuta, *détail de la structure spongieuse ; e)* Branchinecta tolli ; *f)* B. tolli, *détail de la partie déchirée de l'enveloppe ; g)* B. tolli, *détail de la surface montrant les petits tubercules (échelles en* µm).

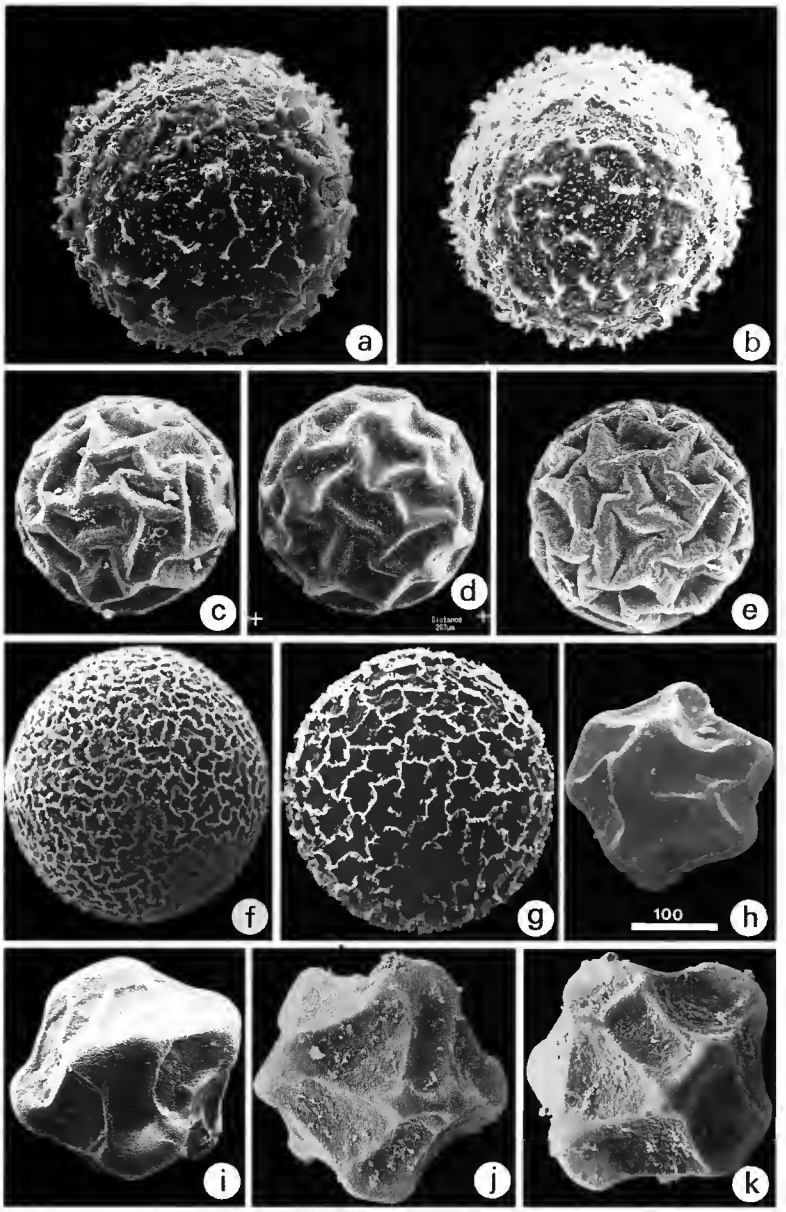

FIG. 6. — Cysts of Anostraca: a), b) *Drepanosurus hankoi*; c), d), e) *Streptocephalus torvicornis*; f), g) *Siphonophanes grubii*; h) *Branchipus schäefferi* syn. *visnyai*; i) *Branchipus schäefferi*; j), k) *Branchipus blanchardi* (common scale bar in µm).

Œufs d'Anostraca : a) et b) Drepanosurus hankoi ; *c), d), e)* Streptocephalus torvicornis ; *f), g)* Siphonophanes grubii ; *h)* Branchipus schäefferi *syn.* visnyai ; *i)* Branchipus schäefferi ; *j), k)* Branchipus blanchardi *(échelle commune en µm).*

ANDERSON, 1988; THIÉRY & GASC, 1991). Except for a small difference in size, no objective distinction exists between the cysts of the parthenogenetic and bisexual strains. The vitelline envelope is thin and spongy (Fig. 7h).

Branchipodidae (Figs 6, 7, 8): this family presents two very different patterns: lenticular cysts in *Tanymastix* (Figs 7g; 8f, g) (only small and often unreliable differences between the species) and wrinkled and angulated in *Branchipus* (Fig. 6h-k). The cysts of *Branchipus schäefferi* and *B. blanchardi* are shown in this paper while that of *B. cortesi* is illustrated in ALONSO & JAUME (1991, Fig. 4b, c, p. 227). As in *Tanymastix*, whose cyst pattern can be considered as generic, the angulated shape of *Branchipus* cysts is so similar in the four European species that we suggest that it could be generic also. This is confirmed by the cyst of *Branchipus laevicornis,* the fifth species of the genus, living in Asia minor, which is very similar in shape to that of the three species studied (Fig. 7d) and that studied by ALONSO & JAUME (1991). The differences between these species are hardly distinguishable without a large series permitting study of the morphology and size variability. This pattern is found also in a thamnocephalid, *Dendrocephalus spartaenovae* (MURA, 1992b, Plate 6.3), but this is a South American species, so no confusion is possible in field studies. In section the alveolar layer of the cyst wall of *Branchipus blanchardi* and *B. laevicornis* (both unpublished), are spongy as in *B. schäefferi* (KUPKA, 1940, Figs 6-11; GILCHRIST, 1978, Figs 1c, d, 2a-d). In addition, the outer surface has numerous pores in *B. blanchardi* (THIÉRY & GASC, 1991, Fig. 32), *B. laevicornis* (unpublished) and *B. schäefferi* (KUPKA, 1940, Fig. 5; GILCHRIST, 1978, Fig. 1b; MURA & THIÉRY, 1986, Pl. IV.B).

Thamnocephalidae (Fig. 8): the cyst of *Branchinella spinosa* is spherical with a surface showing an irregular polygonal pattern formed by low mound-like ridges. These ridges are more or less pronounced (in relation to the maturation of the egg shell). Cyst size is close to that of *Artemia* (which always has smooth cysts), with which this species could coexist in coastal saline waters as in the Camargue and Sardinia. The *B. spinosa* pattern is constant for all populations observed (ALONSO & ALCARAZ, 1984, Fig. 2.d; MURA, 1986, Plate 5.a; 1992b, Plate 1.5; MURA & THIÉRY, 1986, Plate II.a).

Streptocephalidae (Fig. 6): cysts of *Streptocephalus torvicornis* are well known (VALOUSEK, 1952; ALONSO & ALCARAZ, 1984; MURA & THIÉRY, 1986; THIÉRY, 1987; THIÉRY & GASC, 1991; DE WALSCHE *et al.*, 1991; MURA, 1992b). They have a "folded look" with polygonal cells irregularly shaped by raised ridges (Fig. 6c-e). Cysts of *Streptocephalus torvicornis bucheti* are similar to those of *S. t. torvicornis* (ALONSO & ALCARAZ, 1984, and MURA & THIÉRY, 1986).

Linderiellidae (Figs 7, 8): the cysts of the genus *Linderiella* are spiny (Fig. 8d), even with acute spines (15-20 µm long) in the French *Linderiella massaliensis* (Fig. 7f), or with flat trumpet tips in the Spanish form (ALONSO & ALCARAZ, 1984; THIÉRY & CHAMPEAU, 1988). In all cases the spines are different from those of the spiny cysts of some species of *Chirocephalus*, where they arise from the crests of honeycomb-like surface of the shell. In *Linderiella* they arise directly from the shell.

Chirocephalidae Chirocephalinae (Figs 8, 9, 10): at first glance cysts of *Chirocephalus* species present great heterogeneity. Some are smooth, *e.g. Chirocephalus marchesonii* (MURA *et al.*, 1978, Pl. 1; MURA, 1986, Pl. 4), some spiny, *e.g. C. ruffoi* (MURA, 1986, Pl. 12), *C. diaphanus carinatus* (Fig. 9b) and *C. carnuntatus* (Fig. 9i), some more or less bumpy as *C. chyzeri* (Fig. 9c, d),

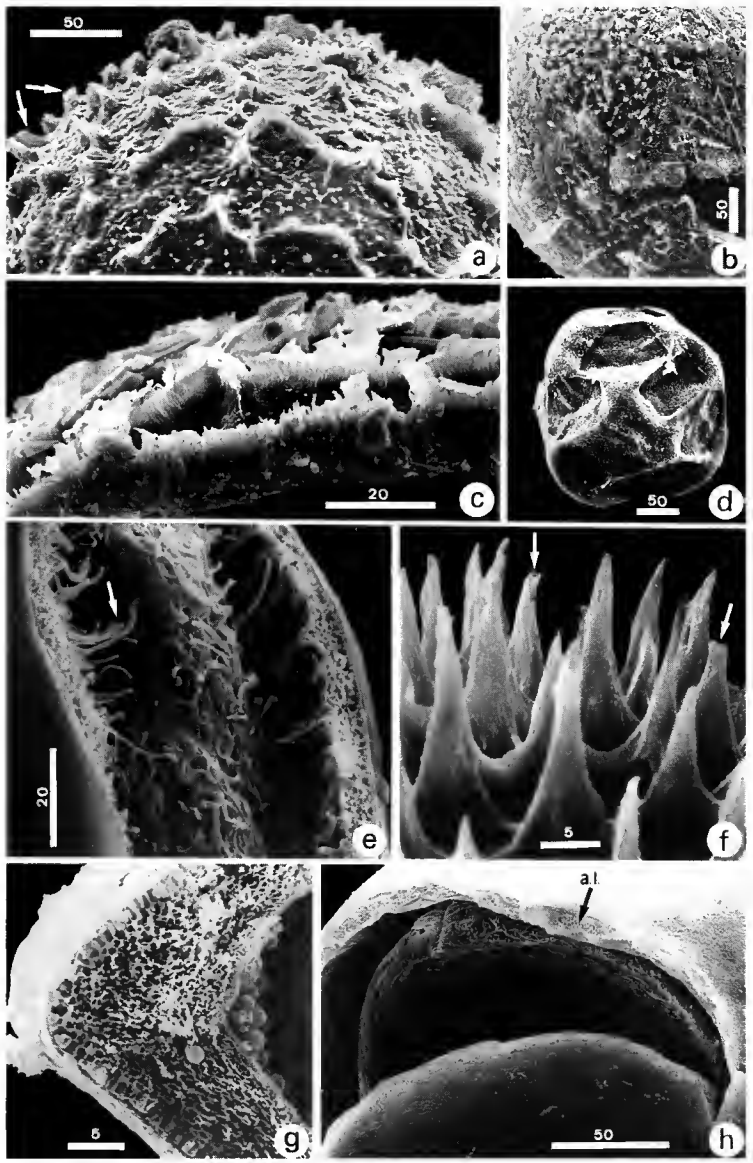

FIG. 7. — Details of the cysts of Anostraca: a) *Drepanosurus hankoi* — see low ridges (arrows); b) *Polyartemia forcipata* — see small spines (arrows); c) *Siphonophanes grubii*; d) whole cyst, *Branchipus laevicornis*; e) internal view of envelope, *Branchinectella media* (see the pillars — arrow); f) spines of *Linderiella massaliensis* (those marked with an arrow are broken), g) section, *Tanymastix stagnalis*, showing spongy structure; h) detail of the envelope, *Artemia* (a.l. — alveolar layer). (Scale bars in µm.)

Détails des œufs d'Anostraca : a) Drepanosurus hankoi — *voir les rides (flèches) ; b)* Polyartemia forcipata — *noter les petites épines (flèches) ; c)* Siphonophanes grubii ; *d) œuf de* Branchipus laevicornis ; *e) vue interne de l'enveloppe chez* Branchinectella media *(noter les filaments — flèche) ; f) épines de* Linderiella massaliensis *(celles marquées d'une flèche sont cassées ; g) coupe transversale de l'œuf de* Tanymastix stagnalis *montrant la structure spongieuse ; h) détail de l'enveloppe d'*Artemia *(a. l. — couche alvéolaire). (Échelles en* µm.)

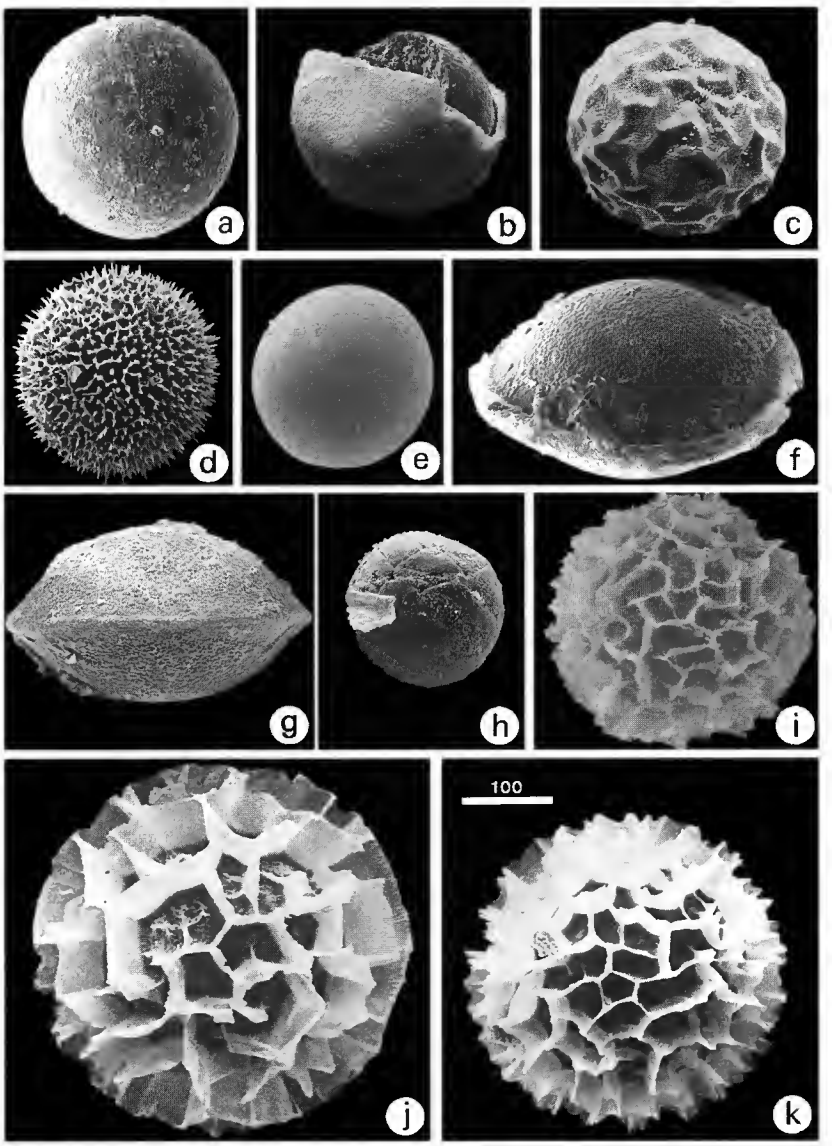

FIG. 8. — Cysts of Anostraca: a) *Artemia* (bisexual strain); b) *idem*, cracked cyst; c) *Branchinella spinosa*; d) *Linderiella massaliensis*; e) *Branchinectella media*; f) *Tanymastix stellae*; g) *Tanymastix stagnalis*; h) immature cyst, *Drepanosurus birostratus*; i) *Chirocephalus orghidani*; j) *Chirocephalus diaphanus*; k) *Chirocephalus salinus* (common scale bar in µm).

Œufs d'Anostraca : Artemia *(souche bisexuée) ; b)* idem, *œuf déchiré ; c)* Branchinella spinosa *; d)* Linderiella massaliensis *; e)* Branchinectella media *; f)* Tanymastix stellae *; g)* Tanymastix stagnalis *; h) œuf immature,* Drepanosurus birostratus *; i)* Chirocephalus orghidani *; j)* Chirocephalus diaphanus *; k)* Chirocephalus salinus *(échelle commune en µm).*

C. slovacicus (Fig. 9e), *C. spinicaudatus* (Fig. 9f), *C. shadini* (Fig. 9g), and *C. josephinae* (Fig. 9h), or have thin and high ridges in *C. orghidani* (Fig. 8i), *C. diaphanus* (Fig. 8j), *C. salinus* (Fig. 8k), and *C. pelagonicus* (Fig. 9a). As far as grouping distinctions are concerned (see BRTEK & THIÉRY, 1995), a typical pattern seems to be dominant in each *Chirocephalus* group. In the *bairdi*-group (4 species), three species (*C. orghidani* – this paper, Fig. 8i; *C. brevipalpis* – PETKOVSKI 1991a, Fig. 1e; and *C. kerkyrensis* – MURA *et al.*, 1978, Pl. 4; MURA, 1986, Pl. 10; 1992b, Pl. 2.1, 2) have a pattern of polygonal areas formed by high and thin crests. This pattern is also present in *Chirocephalus bairdi* (Fig. 10a-c), a species of the Levant. Cysts of the last

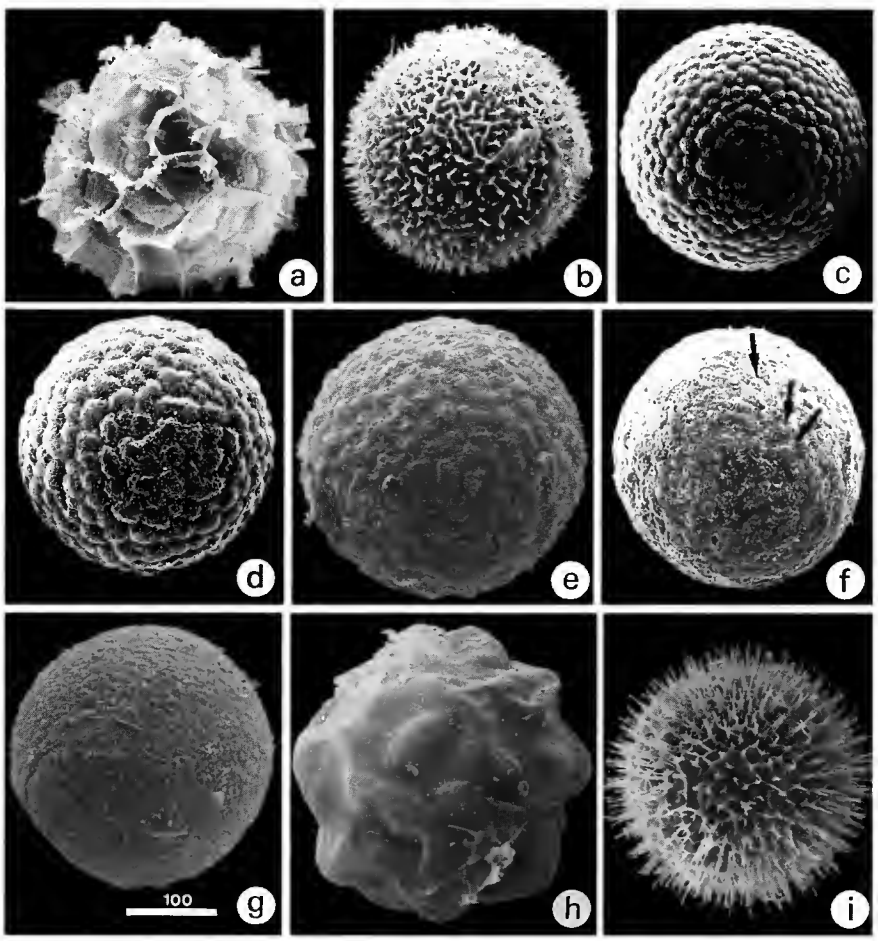

FIG. 9. — Cysts of Anostraca: a) *Chirocephalus pelagonicus*; b) *Chirocephalus diaphanus carinatus*; c), d) *C. chyzeri*; e) *C. slovacicus*; f) *C. spinicaudatus* (note the verucose aspect under the external crust, arrows); g) *C. shadini*; h) *C. josephinae*; i) *C. carnuntanus* (common scale bar in µm).

Œufs d'Anostraca : a) Chirocephalus pelagonicus *; b)* Chirocephalus diaphanus carinatus *; c), d)* C. chyzeri *; e)* C. slovacicus *; f)* C. spinicaudatus *(noter l'aspect verruqueux, flèches) ; g)* C. shadini *; h)* C. josephinae *; i)* C. carnuntanus *(échelle commune en µm).*

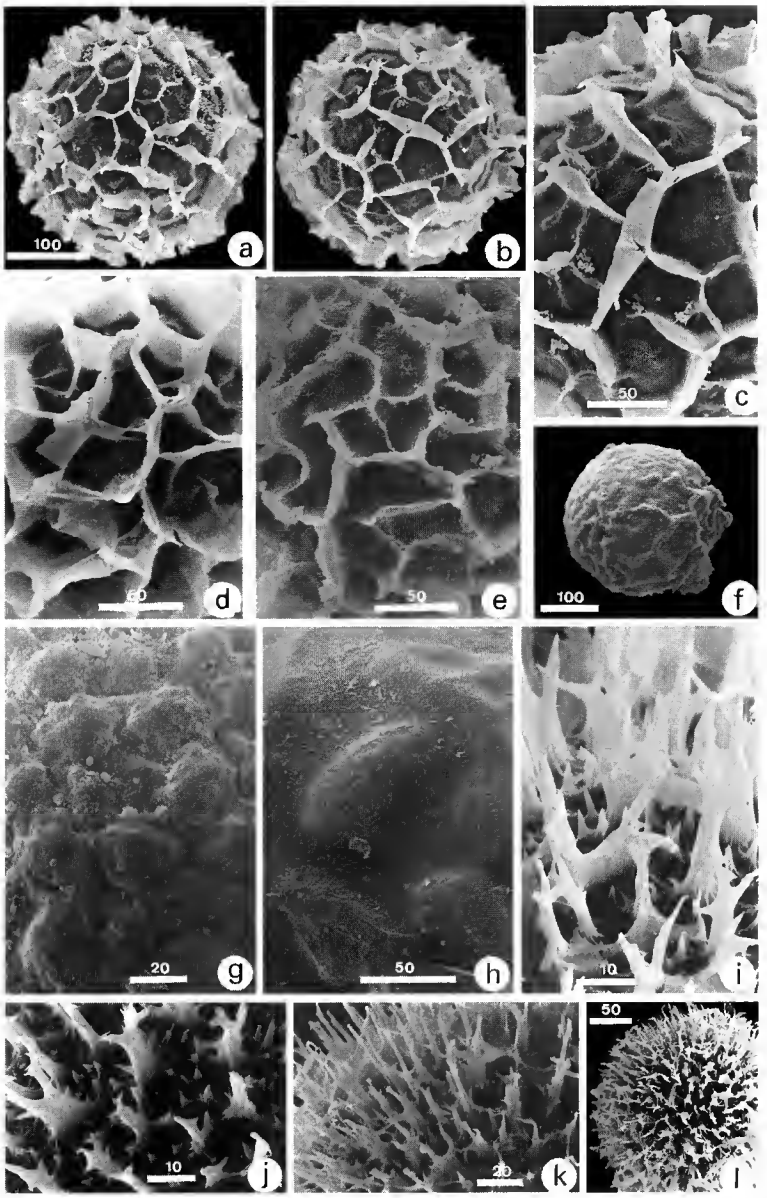

FIG. 10. — Cysts of Anostraca: a), b) *Chirocephalus bairdi*; c) *C. bairdi*, detail of the surface; d) *C. salinus*, detail; e) *C. orghidani*, detail; f) *C. shadini*, (cf. Fig. 9g for minor differences); g) *C. slovacicus*; h) *C. josephinae*; i), j), k),l) spines of *Chirocephalus carnuntanus* (scale bars in µm).

Œufs d'Anostraca : a), b) Chirocephalus bairdi *; c)* C. bairdi, *détail de la surface ; d)* C. salinus, *détail ; e)* C. orghidani, *détail ; f)* C. shadini *(voir fig. 9g pour des petites différences) ; g)* C. slovacicus *; h)* C. josephinae *; i), j), k), l) épines de l'œuf de* Chirocephalus carnuntanus *(échelles en µm).*

species, *C. vornatscheri*, are unknown. In the *diaphanus*-group (8 species), a cyst surface pattern of the type already described for the *bairdi*-group, is found in four species (*C. diaphanus*, *C. salinus*, *C. pelagonicus* – this paper, Figs 8j, k; 9a, and *C. sibyllae* – MURA, 1986, Pl. 9.b, and 1992b, Pl. 2.7). A spiny appearance is observed in two species (*C. diaphanus carinatus* – this paper, and *C. ruffoi* – MURA, 1986, Pls 12 and 13.a, and 1992b, Pl. 2.8, Pl. 5.6), while only one has a smooth aspect (*C. marchesonii* – MURA, 1986, Pl. 4, 1992b, Pl. 2.9). Cysts of *C. reiseri* are unknown. The *pristicephalus*-group (4 species) is more heterogeneous with one spiny cyst (*C. carnuntanus*, Figs 9i; 10i, j, k, l), one slightly verrucose (*C. shadini*, Fig. 9g), or sometimes more verrucose (Fig. 10f). and a cyst clearly bumpy (*C. josephinae*, Figs 9h, 10h). The spines of *Chirocephalus carnuntanus* differ from those of *C. diaphanus carinatus*, *Linderiella massaliensis*, and *C. ruffoi* (see MURA, 1986, Pls 12.b, 13.a) by their length and their "trident" aspect in their distal border (Fig. 10i-k). Cysts of the fourth species, *Chirocephalus ripophilus*, remain unknown. In the *spinicaudatus*-group (6 species), three cysts have a verrucose aspect (*C. spinicaudatus*, Fig. 9f; *C. chyzeri*, Fig. 9c, d; and *C. slovacicus*, Figs 9e; 10g); those of *C. croaticus*, *horribilis*, and *robustus*, are unknown.

Chirocephalidae Eubranchipodinae (Figs 6, 7, 8): cysts of *Drepanosurus hankoi* are spherical with irregular, unconnected low ridges or vertical lamellae, 10-15 µm high, non converging and situated without any regularity (Fig. 7a). The surface is also rugose. This pattern is described by MURA (1992b, Plate 5.2). As we could study the cyst of only one of the three European species of *Drepanosurus*, nothing can be said about the generic pattern, but we can note that the pattern found in *D. hankoi* agrees with DADAY's description (1910, Fig. 33g, 1, p. 244) of *D. birostratus* whose cysts are *ova superficie spinulosa, spinulis bacilliformibus*. The cysts of *D. birostratus* described in the present study (Fig. 8h) are immature. No data are available for *D. vladimiri*.

Cyst of *Siphonophanes grubii* somewhat resemble those of *Drepanosurus hankoi* but with thin wrinkled low ribs, connected to one another (Fig. 6f, g), and arranged in a dense complex coral-like network delineating small irregular areas. The wrinkled ribs are 14-17 µm high (Fig. 7c). (see earlier descriptions made by THIÉRY & GASC, 1991, Fig. 14, and MURA, 1992b, Plate 5.1.

Chirocephalidae Branchinectellinae (Figs 7, 8): cysts of *Branchinectella media* are smooth (Figs 7e; 8e; ALONSO & ALCARAZ, 1984, Fig. 2.e) and superficially similar to those of *Artemia*. The structure of the shell, however, is clearly different, with an inner alveolar layer which consists of vertical strands approximately 15 µm long and 1-2 µm thick (Fig. 7e), while in *Artemia* it is only spongy (Fig. 7h).

NOTOSTRACA. Triopsidae (Figs 11, 12): cysts are spherical with a smooth or finely rugose surface. Only the diameter can be used in identification but variation within each species (V. I. from 13 to 26%), makes distinction difficult, particularly between *Triops cancriformis* and *Lepidurus couesii* or between *Lepidurus couesii* and *L. apus*.

Notostracans have the largest resting eggs with spherical cyst up to 400 µm in diameter (Fig. 12). *Triops cancriformis*, *Lepidurus couesii* and *L. apus* have the smallest cysts with respectively diameters of 350-400 µm, 425 µm and 430-520 µm. *Lepidurus arcticus* cysts are larger (603-621 µm) and have a rough surface while those of *Lepidurus apus*, *L. couesii* and *Triops cancriformis* are smooth (Figs 11, 12). The alveolar envelope is also thinner than in other

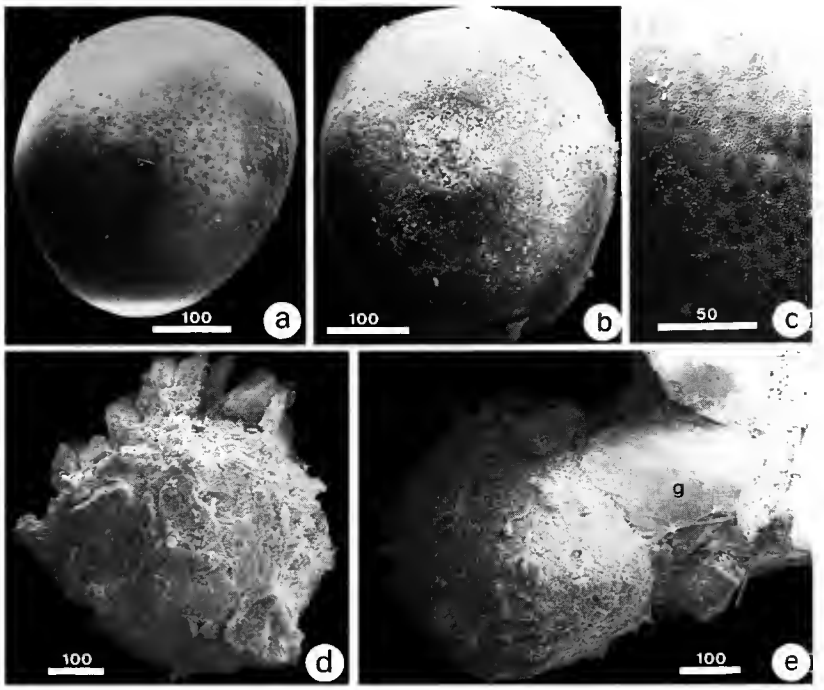

FIG. 11. — Cysts of Notostraca: a), b) *Triops cancriformis*; c) *idem*, detail of surface; d) *idem*, cysts stuck on gravel; e) *Lepidurus apus*, cyst stuck on gravel (g). (Scale bars in µm.)

Œufs de Notostraca : a), b) Triops cancriformis *; c)* idem, *détail de la surface ; d)* idem, *œuf collé à des graviers ; e)* Lepidurus apus, *œuf collé sur un gravier (g). (Échelles en µm.)*

notostracans (from 25 to 70 µm) while the alveolar layer reaches sometimes 110 µm. As reported by THIÉRY (1985) and FRYER (1988) cysts are mostly covered with sediments and gravels (Fig. 11d, e).

Cysts of the Afro-Asian *Triops numidicus*, penetrating Europe only in Sicily and Majorca, is not illustrated here. A description is given in THIÉRY (1985, 1995), and THIÉRY (in press) (spherical and smooth cyst, diameter 610-740 µm).

SPINICAUDATA (Figs 13, 14). Cyzicidae (Fig. 13): cysts of *Cyzicus* species are spherical, smooth with a very thin membrane (< 2 µm) covering a network of thin radiating and entangled setules (Fig. 13f, g, i) approximately 0.4 µm thick and 10-15 µm long (= the vitelline envelope *sensu* TOMMASINI & SCANABISSI SABELLI, 1989). The membrane is sometimes cracked (Fig. 13f, i) allowing the setose envelope to be observed without any treatment. As discussed by THIÉRY & GASC (1991) and THIÉRY (1995), this egg shell structure can be considered generic. For other descriptions of *Cyzicus* cysts see DADAY (1914: *Cyzicus tetracerus*); ALONSO & ALCARAZ (1984: *Cyzicus grubei*), THIÉRY (in press: *Cyzicus gihoni*), and THIÉRY (in prep.: *Cyzicus bucheti*).

Eocyzicus has a different egg shell pattern. The external surface of *E. orientalis* cyst is bumpy (Fig. 13h, j), as described by DADAY (1914: *Ova membrana concinne granulata tecta*).

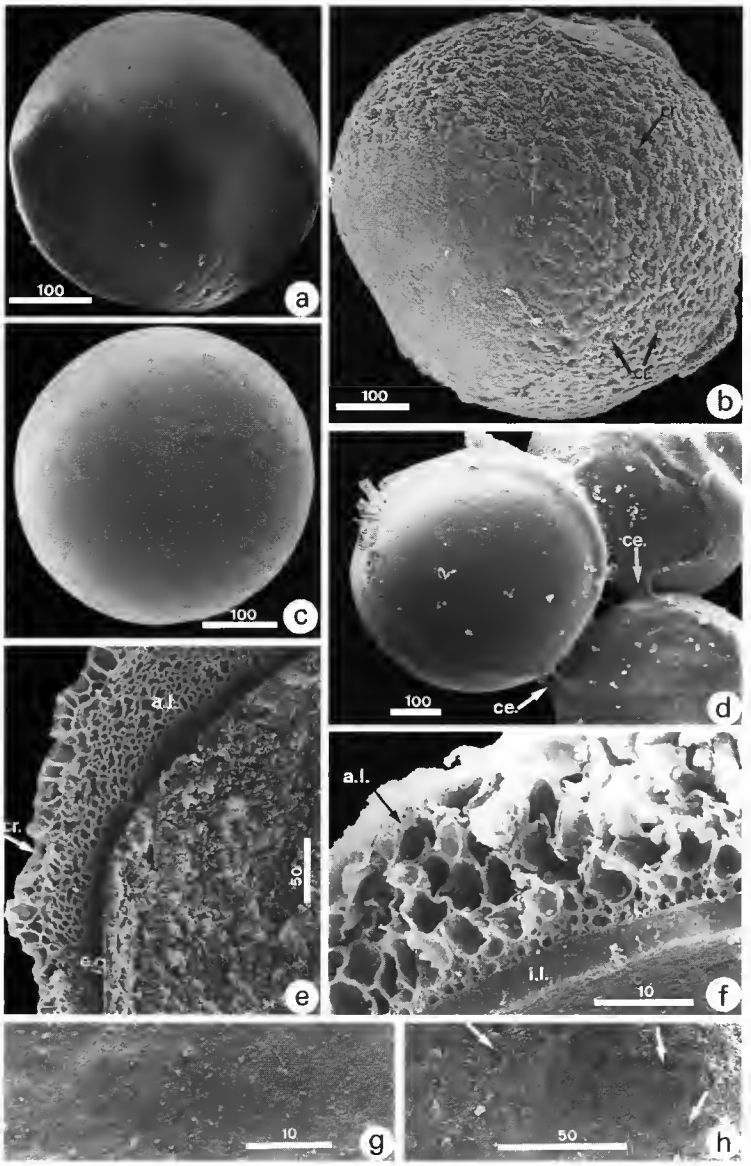

FIG. 12. — Cysts of Notostraca: a) *Lepidurus apus*; b) surface of the cyst of *Lepidurus arcticus* with numerous craters (cr.), c) *Lepidurus couesii*; d) cysts of *Lepidurus apus* glued together by cement (ce.); e) *L. arcticus*, cross section of wall showing alveolar layer (a.l.), embryonic cuticle (e.c.), crater (cr.); f) *L. apus*, section of cyst wall with alveolar layer (a.l.), inner layer (i.l.); g), h) surface of *L. apus* cysts showing in h) the obliterated craters (arrows). (Scale bars in µm.)

Œufs de Notostraca : a) Lepidurus apus ; *b)* Lepidurus arcticus, *noter la présence de cratères (c.r.) en surface ; c)* Lepidurus couesii *; d) œufs de* Lepidurus apus *agglutinés par un cément (ce.) ; e)* L. articus, *coupe transversale de la paroi montrant la couche alvéolaire (a.l.), la cuticule embryonnaire (e.c.) et les cratères (cr.) ; f)* L. apus, *coupe transversale de la paroi, couche alvéolaire (a.l.), couche interne (i.l.) ; g), h) surface des œufs de* L. apus *montrant (en h)) des cratères oblitérés (flèches). (Échelles en µm).*

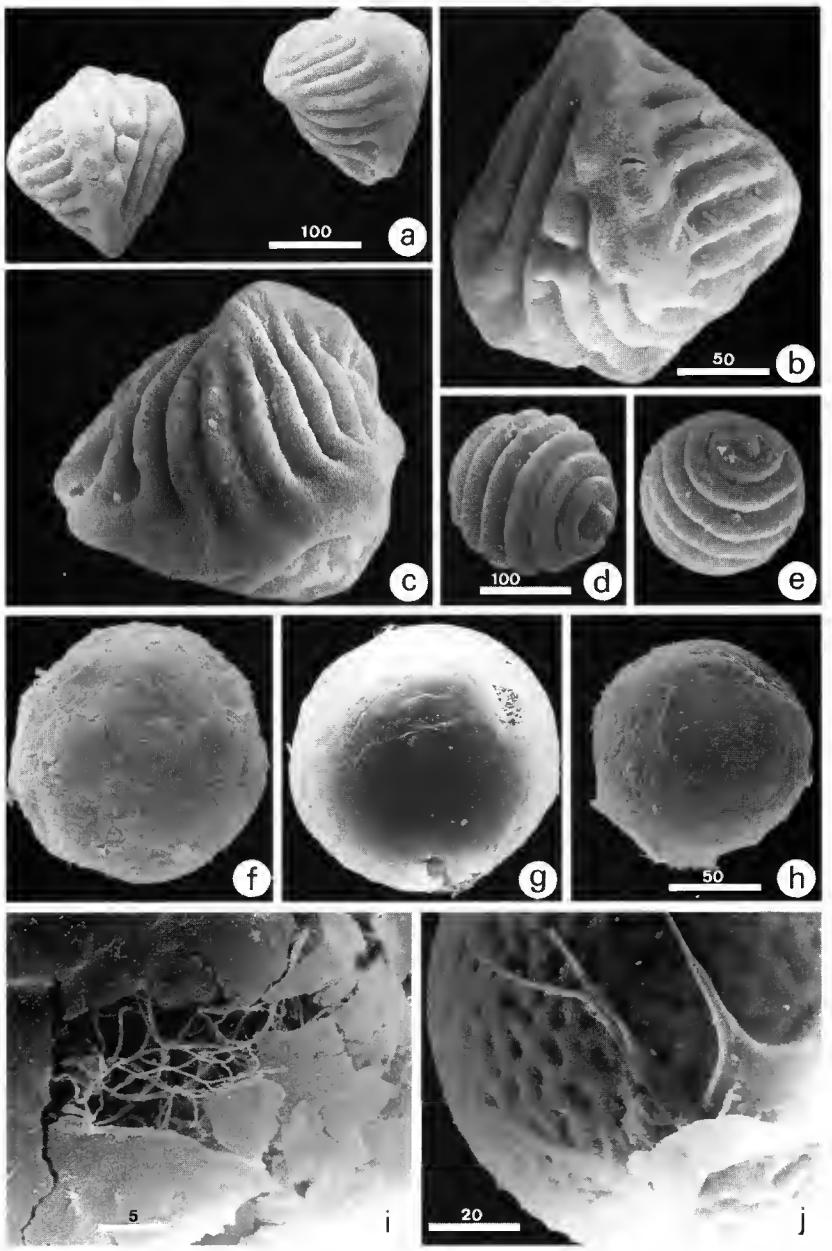

FIG. 13. — Cysts of conchostracans (Spinicaudata): a), b), c) *Limnadia lenticularis* (b), c): same scale), d), e) *Imnadia yeyetta* (same scale); f), g) *Cyzicus tetracerus*; h) *Eocyzicus orientalis* (f), g), h): same scale), i) cracked egg shell, *C. tetracerus*; j) outer surface, *E. orientalis*. (scale bars in µm).

Œufs de conchostracés (Spinicaudata) : a), b), c) Limnadia lenticularis *(b), c) : même échelle) ; d), e)* Imnadia yeyetta *(même échelle) ; f), g)* Cyzicus tetracerus *; h)* Eocyzicus orientalis *(f), g), h) : même échelle) ; i) enveloppe externe déchirée de* C. tetracerus *; j) surface externe de* E. orientalis *(échelles en µm).*

A similar pattern has been described for other species of the genus by SAMYIAH *et al.* (1985: = *Caenestheriella*), and THIÉRY (1987; 1995). Cysts of *Eocyzicus propinqus*, *E. skorikowi* and *E. tadei* were not available for our study.

Leptestheriidae (Fig. 14): cysts of *Leptestheria* and *Eoleptestheria* are spherical and smooth with no clearly distinct differences (Fig. 14a-d). Species and genera of this family may be separated by adult characters only. The cyst pattern of several species of the Leptestheriidae – small with a smooth surface – has already been presented by BOTNARIUC (1947, Pl. I, Fig. 7: *Leptestheria intermedia*), THIÉRY (1987, 1995: *Leptestheria mayeti*), TOMMASINI & SCANABISSI SABELLI (1989, Figs 11, 12: *Leptestheria dahalacencis*), and BRENDONCK *et al.* (1993: *Leptestheria aegyptiaca*).

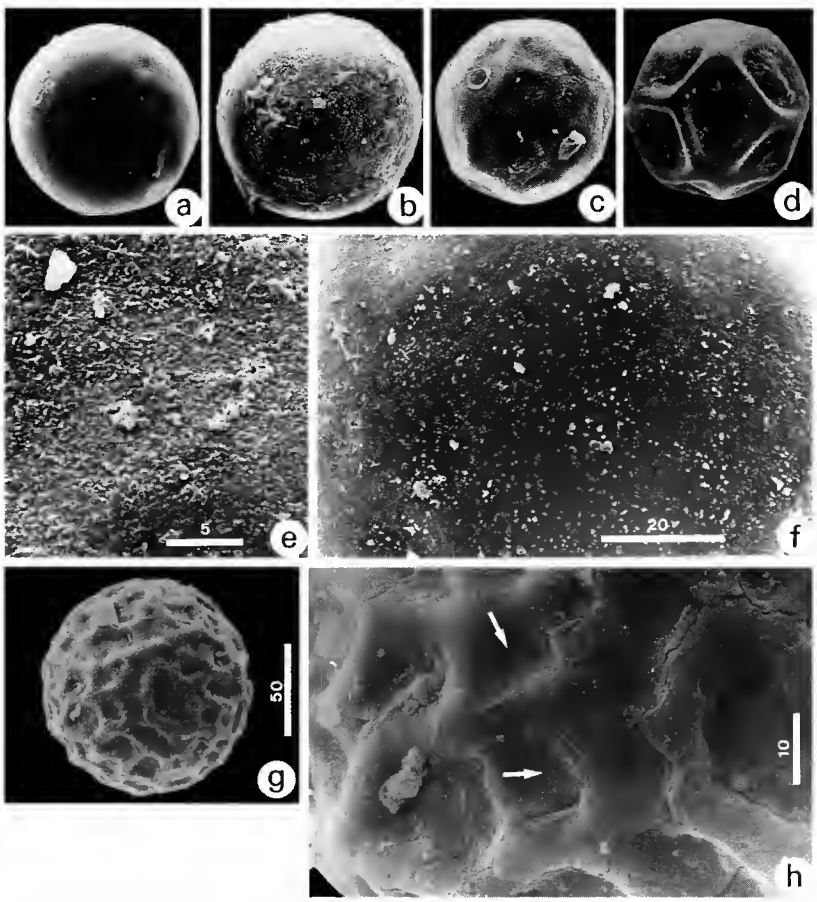

FIG. 14. — Cysts of conchostracans (Spinicaudata and Laevicaudata): a)-c) *Leptestheria dahalacencis*; d) *idem*, not fully mature cyst deformed by preparation for scanning; e) *idem*, surface; f) detail of surface, *Eoleptestheria ticinensis*; g) *Lynceus brachyurus*; h) same species, detail of the surface showing depressions (arrows). (a)-d), g): same scale.) (Scale bars in µm.)

Œufs de conchostracés (Spinicaudata et Laevicaudata) : a)-c) Leptestheria dahalacencis*; d)* idem*, œuf immature déformé par la préparation pour le scanning ; e)* idem*, surface ; f) détail de la surface chez* Eoleptestheria ticinensis*; g)* Lynceus brachyurus*; h) même espèce, détail des dépressions de surface (flèches). (a)-d), g): même échelle.) (Échelles en µm.)

LIMNADIIDAE (Fig. 13): cysts of *Limnadia* and *Imnadia* are now well known (THIÉRY & GASC, 1991). The present material supplies additional pictures but no new information. In *Limnadia*, the cyst is clam-shell like and biconcave with ridges converging to an apical point (Fig. 13a-c), so that MARTIN (1989) called them "twisted eggs". No objective difference could be observed between the cysts of American populations described by MARTIN (1989) and those of European populations described by SARS (1896), DADAY (1925), ZAFFAGNINI (1967), and THIÉRY & GASC (1991).

Imnadia cysts have a spiral aspect (Fig. 13d, e), as illustrated by BOTNARIUC (1947), BTREK (1957, Fig. 2h), and THIÉRY & GASC (1991). In both *Limnadia* and *Imnadia* the cyst patterns are unique in the "large branchiopods" and can be considered as generic.

LAEVICAUDATA (Fig. 14): cysts of *Lynceus brachyurus* are spherical and look like a small golf-ball with more or less angular depressions (Fig. 14g, h). They are among the smaller cysts of European phyllopods (approximately 120 µm). Cysts of *Lynceus andronachensis* illustrated by BOTNARIUC (1947, Pl. I, Fig. 15) resembles those of *L. brachyurus*.

DISCUSSION

From our observations, complemented by reliable data in the literature, it appears that the species present a relatively constant morphology of the mature cysts over their whole distributional area. However, the fact that the surface pattern and size sometimes presents relative variability is hardly discussed by MURA (1991a, 1992a, b). In the case of phyllopods it is true that several species, occupying a large distribution area, present more or less important differences in size between populations of different habitats particularly between those in lowlands and high mountains (THIÉRY, 1987, in prep.; BELK *et al.*, 1990; MURA, 1991b). In these cases the size is statistically different but the external pattern remains quite similar.

When species have cysts with similar surface patterns, their size usually allows their identification. When the two characters are unable to allow a clear distinction, it is useful to consider the structure of the shell, as in the case of *Artemia* and *Branchinectella media* (spongy *vs* roots/pillars). Only a small number of species have markedly similar cysts (*Leptestheria* and *Eoleptestheria* in the Leptestheriidae, *Branchinecta paludosa* and *B. ferox*, the different species of the genus *Tanymastix*, and several notostracans). In the case of *Branchinecta orientalis* and *B. minuta*, the fact that the cysts closely resemble each other in pattern and size raises the question of an eventual synonymy, as was the case for *Branchipus blanchardi* and *B. alpinus* (see the respective cysts in MURA, 1986, Pl. 13b, and THIÉRY & GASC, 1991, Figs 16, 28).

For about 80% of the European species, the combination of surface pattern/size is a valid means of species identification. In some other cases, *e.g. Tanymastix, Branchipus*, *Cyzicus*, cyst morphology presents only a generic peculiarity.

As observed in most of species of Anostraca (HELLSTRÖM & NAUWERCK, 1971; THIÉRY, 1987), the number of resting eggs is related to the length of the female. Except some cases (BELK *et al.*, 1990), the size of cysts is usually approximately constant from the first to last batches (BELK, 1977; MURA, 1991b). Considering the absolute value of the size of the cysts within the Anostraca, Notostraca, Spinicaudata and Laevicaudata, our study allows us to

distinguish three groups: notostracans with eggs larger than 450 µm, conchostracans with eggs less than 200 µm, and, between these groups anostracans with cysts from 250 to 450 µm. This is in accord with the gradient found by THIÉRY (1987) for Moroccan "large branchiopods", by THIÉRY & GASC (1991) for French species, and by BRENDOCK *et al.* (1993) for tropical African species.

Our study needs, however, to be completed by the description of cysts of species which are lacking in this paper (lack of material such as *Chirocephalus ripophilus*, *C. robustus*, *C. reiseri*, *C. horribilis*, or immature cysts such as in the case of *Drepanosurus birostratus*). Also, even though egg morphology seems to be a useful species- or genus-specific character, the full extent of its taxonomic value in some cases remains limited. Some cysts of different species are very similar. Despite cases which are the subject of conflicting opinions, cyst morphology, shape, and size taken together often represent a useful adjunct to identification which should be included along with classical species descriptions, as was done for example by MAEDA-MARTINEZ *et al.* (1992, 1993), and SMITH (1992). However, the choice of cysts (maturity level) and measurements need stringent attention, to avoid the confusions or errors (erroneous scale bars) which cause some data to be unusable. (Errors and omissions found in all references about cysts are noted in Table I).

Cyst data also provide additional support for the close relationship recognized between certain anostracans on other grounds by DADAY (1910). For example, in the Chirocephalidae, if the cyst morphology pattern of different species follows in part the groups determined on classical characters of the male (antennae, penes), it is sometimes discordant (*e.g.* the heterogenous *Pristicephalus*-group). In consequence it will be interesting to study large series of cysts from different populations to prove or disprove statistically that the size of cysts is more or less constant and not correlated with the length/age of the female. It will be also useful to consider whether size is linked with altitude, as in *Triops cancriformis* and *Chirocephalus diaphanus* in Morocco (THIÉRY, 1987), or in *Chirocephalus* in Italy (MURA, 1991b).

Finally, the morphological study of cysts has reached its limits and needs to be completed by biochemical studies which may provide insights into the formation of so great a variety of egg shells in the "large branchiopods" (spiny, bumpy, lenticular, spiral, twisted, smooth, etc.). Research dealing with this subject, previously discussed by THIÉRY (1987, p. 338), is in progress. We think also that isoelectric focusing data could help to clarify the taxonomy of several families, the Chirocephalids for example. This technique could also measure the genetic distance between the five endemic species of *Branchipus*, the genetic distance between the Linderiellidae and Chirocephalidae, between *Leptestheria* and *Eoleptestheria*, and help determine a hierarchy in characters (importance of the cyst *vs* penes, or antennae). We will use biochemical methods which were initiated in anostracan studies by SIEDEL & SIMPSON (1984), NAVARRO *et al.* (1987), REQUINTINA & SIMPSON (1987), FUGATE (1992), THIÉRY & FUGATE (1994), for more extensive research.

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TABLE 1. — Recapitulative list of cyst measurements of European "phyllopods". Species cited in the checklist of BRTEK & THIÉRY (1995) which are not in this table have cysts which remain unknown. n = number of measured cysts, V. I. = variation index, S = standard error, $\bar{x}$ = mean. The symbol /?/ in the column of measurements indicates that the value is doubtful, corresponding most of the time to a scale-bar error.

Liste récapitulative des mesures des œufs des espèces de « phyllopodes » actuellement connues en Europe. Les œufs des espèces citées dans la liste de BRTEK & THIÉRY (1995) *qui ne sont pas dans ce tableau ne sont pas connus. n = nombre d'œufs mesurés, V. I. = indice de variation (en %), $\bar{x}$ = moyenne, S = erreur standard. Le symbole /?/ dans la colonne des mesures indique que la valeur tirée d'une référence bibliographique est douteuse, la plupart du temps suite à une erreur d'échelle.*

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
ANOSTRACA			
Polyartemia forcipata	527 µm (n = 1)	This study	Russia
(V. I. = 15.76 %)	0.45 mm	HELLSTRÖM & NAUWERCK (1971)	Sweden
Branchinecta ferox	386 - 412 µm (n = 6)	This study	Slovakia
(V. I. = 24.61 %)	352 - 383 µm (n = 3)	This study	Slovakia
	0.36 - 0.42 mm	ALONSO (1985)	Spain
	error in scale	ALONSO & ALCARAZ (1984)	Spain
	438 µm	MURA & THIÉRY (1986)	Morocco
	342 µm	PETKOVSKI (1991*b*)	Yugoslavia
	0.241 mm (cysts clearly immature)	CÉSAR (1989)	MHN Paris without reference
Branchinecta minuta	290 - 305 µm (n = 3)	This study	Russia

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
Branchinecta orientalis	277 - 280 µm (n = 2)	This study	Austria
(V. I. = 37.40 %)	219 µm	Alonso & Alcaraz (1984)	Spain
	0.22 - 0.32 mm	Alonso (1985)	Spain
	263 µm	Petkovski (1991*b*)	Yugoslavia
Branchinecta paludosa	394 - 442 µm (n = 3)	This study	Slovakia
(V. I. = 47.64%)	264 µm /?/	Mura (1991*a*)	North America
	320 - 325 µm (n = 15)	This study	Russia
	0.396 mm	César (1989)	MNHN Paris without reference
	0.27 - 0.38 mm ($\bar{x}$ = 0.35 mm, n > 30)	Belk (1977)	USA-Arizona
Branchinecta tolli (V. I. = 7.43 %)	311 - 335 µm (n = 7)	This study	Russia
Artemia parthenogenetica	216 - 269 µm [$\bar{x}$ = 240.3 µm, SD = 18.43, n = 10]	This study	France
(V. I. = 27.51 %)	220 - 270 µm	Thiéry & Gasc (1991)	France
	241.2 µm	Videla & Castela Branco (1987)	Portugal
	259 µm	Vanhaecke & Sorgeloos (1980)	France
	266 µm (n = 50)	Vieira & Amat (1985)	Portugal
	238.8 µm	Thiéry & Robert (1992)	France
	251.8 - 263.1 µm	Castritsi - Catharios *et al.* (1987)	Greece
	260.1 - 264.7 µm (n = 500)	Abatzopoulos *et al.* (1987)	Greece
	270.1 - 279.3 µm (in laboratory culture)	Abatzopoulos *et al.* (1987)	Greece
	208 - 234 µm (n = 14)	Thiéry (in press)	Saudi Arabia
	15.3 - 28.9 µm /?/ ($\bar{x}$ = 24.1 µm)	Majic & Vukadin (1987)	Yugoslavia
	259.6 µm	Vanhaecke & Sorgeloos (1980)	France (Aigues-Mortes)
	276.3 µm	Vanhaecke & Sorgeloos (1980)	France (Lavalduc)
	264.4 µm	Vanhaecke & Sorgeloos (1980)	France (Salins de Giraud)
	257.8 µm	Vanhaecke & Sorgeloos (1980)	France (Salins d'Hyères)
	253.6 µm	Vanhaecke & Sorgeloos (1980)	Spain
	284.9 µm	Vanhaecke & Sorgeloos (1980)	Italy

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
	0.20 - 0.25 mm	MATHIAS (1937)	France
	255.39 µm (n = 655)	TRIANTAPHYLLIDIS *et al.* (1993)	Greece Lesbos Island-Kallon
	269.71 µm (n = 777)	TRIANTAPHYLLIDIS *et al.* (1993)	Greece Lesbos Polychnitos
Artemia tunisiana	208 - 286 µm (n = 5)	This study	France (Sète)
(bisexual)	231.2 - 268.0 µm	VIDELA & CASTELA BRANCO (1987)	Portugal
(V. I. = 31.57 %)	245 µm	Thiéry & Gasc (1991)	France (Sète)
	245.3 µm	Thiéry & Robert (1992)	France (Sète)
	222-234 µm (probably a New World bi-sexual strain-not *A. tunisiana*)	MAILLARD & BAUDET (1980)	France (Guérande)
Branchipus blanchardi	288 - 290 µm (n = 3)	This study	France (Alps-Cristol plateau)
(V. I. = 19.18 %)	300 µm	THIÉRY & GASC (1991)	France (Alps-Cristol plateau)
	# 0.35 mm	ALONSO (1989)	France (Alps)
	291 µm	MURA (1986)	Italy (Alps)
Branchipus cortesi	0.25 mm	ALONSO & JAUME (1991)	Spain
Branchipus intermedius	200 µm	ORGHIDAN (1947)	Romania
Branchipus schäefferi	228 - 270 µm (n = 5)	This study	France (Languedoc)
(V. I. = 42.36 %)	205 - 250 µm (n = 4)	This study	France (Crau)
	238 - 253 µm (n = 4) syn. *visnyai*	This study	Slovakia
	254 µm - syn. *visnyai*	MURA (1986)	Italy
	195 µm	KUPKA (1940)	not indicated
	0.25 mm	GILCHRIST (1978)	not indicated
	0.2 - 0.3 mm	ALONSO (1985)	Spain
	0.2 - 0.28 mm	MATHIAS (1937)	not indicated
	320 µm /?/	MURA (1986)	Italy
	253 µm	MURA & THIÉRY (1986)	Morocco
	260 - 289 µm (n = 10)	THIÉRY (1995)	Saudi Arabia
Tanymastix motasi	0.35 mm	PETKOVSKI (1995)	Macedonia
Tanymastix stagnalis	300/313 -192/195 µm (n = 5)	This study	France
(V. I. = 55.52 %)	0.233 / 0.164 mm	GARREAU DE LOUBRESSE (1982)	France
	337.8 µm	ALONSO & ALCARAZ (1984)	Spain
	0.40 - 0.43 mm	ALONSO (1985)	Spain

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
	0.43 mm	AL-TIKRITY & GRAINGER (1990)	Ireland
	0.35 - 0.40 mm	PETKOVSKI (1995)	Macedonia
Tanymastix stellae	370 µm	CHAMPEAU & THIÉRY (1990)	Corsica
	485 µm /?/	MURA (1986)	Sardinia
Branchinella spinosa	250 - 260 µm	MURA (1992*b*)	Italy
(V. I. = 15.35 %)	260.1 µm	THIÉRY & GASC (1991)	France (Camargue)
	223 µm	MURA & THIÉRY (1986)	Morocco
	224 µm	MURA (1986)	Italy
	225 - 235 µm	THIÉRY (in press)	Saudi Arabia
Streptocephalus torvicornis torvicornis	263 - 279 µm (n = 3)	This study	Slovakia
(V. I. = 42.76 %)	0.3 mm	VALOUSEK (1952)	Czechoslovakia
	0.22 - 0.33 mm	ALONSO (1985)	Spain
	250 µm	ALONSO & ALCARAZ (1984)	Spain
	240 µm	MURA (1992*a*)	Origin not indicated
	231 - 239 µm (n = 8)	THIÉRY (1995)	Saudi Arabia
	0.22 mm	ZOGRAF (1907)	Russia
Streptocephalus torvicornis bucheti	244.3 µm	ALONSO & ALCARAZ (1984)	Spain
(V. I. = 12.29 %)	276.3 µm	MURA & THIÉRY (1986)	Morocco
Linderiella massaliensis (V. I. = 8.0 %)	240 - 260 µm	THIÉRY & GASC (1991)	France
Linderiella sp. (V. I. = 12.24 %)	0.23 - 0.26 mm	ALONSO (1985)	Spain
	255 µm	ALONSO & ALCARAZ (1984)	Spain
Chirocephalus brevipalpis	(316 µm from fig.1.e, but the text indicates 0.22 - 0.24 mm)	PETKOVSKI (1991*a*)	Yugoslavia
	(erroneous scale bar in the figure, Petkovski, ab ora)		
Chirocephalus carnuntanus	240 - 260 µm (n = 4)	This study	Slovakia
	0.154 mm (immature cyst)	ZOGRAF (1907)	not indicated
Chirocephalus chyzeri	259 - 310 µm (n = 5)	This study	Slovakia
Chirocephalus diaphanus	370 - 429 µm (n = 6)	This study	Slovakia
(V. I. = 52.08 %)	360 - 420 µm	THIÉRY & GASC (1991)	France
	340 µm	ALONSO & ALCARAZ (1984)	Spain

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
	287 µm	MURA *et al.* (1978)	Italy
	0.25 - 0.32 mm	ALONSO (1985)	Spain
	0.43 mm	HALL & MAC DONALD (1975)	England
	270 µm	POISSON *et al.* (1946)	France
	0.25 mm	MATHIAS (1937)	not indicated
	error in scale	MURA (1992*b*)	Italy
Chirocephalus diaphanus carinatus	270 - 288 µm (n = 9)	This study	Bulgaria
Chirocephalus josephinae	331 - 345 µm (n = 3)	This study	Russia
	0.25 mm	ZOGRAF (1907)	Russia
Chirocephalus kerkyrensis	266 - 331 µm	MURA (1986)	Italy
(V. I. = 21.48 %)	error in scale	MURA (1992*b*)	Italy
	311 µm (n = 50)	MURA *et al.* (1978)	Italy
Chirocephalus marchesoni	428 µm (n = 50)	MURA *et al.* (1978)	Italy
	363 µm	MURA (1986)	Italy
	error in scale	MURA (1992*b*)	Italy
Chirocephalus orghidani (V. I. = 5.99 %)	275 - 292 µm (n = 3)	This study	Roumania
Chirocephalus pelagonicus	295 - 296 µm (n = 2)	This study	Yugoslavia
(V. I. = 12.10 %)	333 µm	PETKOVSKI (1986)	Yugoslavia
Chirocephalus ruffoi	252 µm	MURA (1986)	Italy
	no scale	COTTARELLI & MURA (1984)	Italy
	error in scale	MURA (1992*b*)	Italy
Chirocephalus salinus	345 - 363 µm (n = 4)	This study	Corsica
	341 - 360 µm (n = 4)	THIÉRY & GASC (1991)	Corsica
	355 µm	CHAMPEAU & THIÉRY (1990)	Corsica
	256 µm /?/	MURA *et al.* (1978)	Sardinia
	362 µm	MURA (1986)	Sardinia (code 600)
	256 µm /?/	MURA (1986)	Sardinia (code 300)
	error in scale	MURA (1992*b*)	not indicated
Chirocephalus shadini	275 - 280 µm (n = 6)	This study	Slovakia
Chirocephalus slovacicus	311 - 325 µm (n = 3)	This study	Slovakia
(V. I. = 10.52 %)	306 - 332 µm (n = 5)	This study	Slovakia
	329 - 340 µm (n = 3)	This study	Slovakia

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
Chirocephalus spinicaudatus	264 µm	This study	France (MNHN Paris Bp. 157)
Chirocephalus sibyllae	290 µm	Mura (1986)	Italy
	error in scale	Mura (1992*b*)	Italy
Drepanosurus birostratrus	173 µm, but immature cyst	This study	Russia
Drepanosurus hankoi	341 - 358 µm (n = 5)	This study	Slovakia
	300 µm	Mura (1992*b*)	origin not indicated
Siphonophanes grubii	353 µm (n = 1)	This study	Slovakia (MNHN Paris Bp. 260)
(V. I. = 16.23 %)	0.30 - 0.33 mm	Buchholz (1864)	Germany
	312 µm	Mura (1992*b*)	not indicated
Branchinectella media	198 - 211 µm (n = 3)	This study	Russia
(V. I. = 6.36 %)	208.6 µm	Alonso & Alcaraz (1984)	Spain
	0.2 mm	Alonso (1985)	Spain
NOTOSTRACA			
Lepidurus apus	436 - 485 µm (n = 5)	This study	France (Provence) - dried
(V. I. = 26.08 %)	432 - 495 µm (n = 12)	This study	South-France (Gavoti)
	455 - 471 µm (n = 4)	This study	France (Languedoc)
	496 µm (n = 1)	This study	Slovakia
	0.4 - 0.5 mm	Alonso (1985)	Spain
	479 µm	Alonso & Alcaraz (1984)	Spain
	0.6 mm	Réau de la Gaignonnière (du) (1908)	France (Angers)
	440 µm	Arnoult (1951)	France (Toulouse)
	0.4 - 0.6 mm	Mathias (1937)	not indicated
	430 - 520 µm	Thiéry & Gasc (1991)	France
Lepidurus couesii	420 - 425 µm (n = 3)	This study	Mongolia
Lepidurus arcticus	603 - 621 µm (n = 3)	This study	Russia
(V. I. = 14.78 %)	0.7 mm	Braem (1893)	not indicated
	700 µm	Fryer (1988)	Iceland
Triops cancriformis	350 - 380 µm (n = 3)	This study	Slovakia
(V. I. = 16.21 %)	368 - 372 µm (n = 6)	This study	France (Opoul)
	355 - 375 µm (n = 4)	This study	France (Crau)
	0.37 mm	Gilchrist (1978)	England
	360 - 400 µm	Thiéry & Gasc (1991)	France (Languedoc)
	0.4 - 0.6 mm /?/	Mathias (1937)	France
	0.34 mm	Tommasini *et al.* (1989)	Italy

SPECIES	CYST MEASUREMENTS [mini - maxi or mean (n =)]	REFERENCE IN LITERATURE	LOCALITY
Triops cancriformis mauritanicus	423 µm	Alonso & Alcaraz (1984)	Spain
(V. I. = 18.98 %)	442 - 510 µm	Thiéry (1987)	Morocco
Triops cancriformis simplex	391 µm	Alonso & Alcaraz (1984)	Spain
(V. I. = 5.52 %)	370 µm	Thiéry (1987)	Morocco
Triops numidicus	1 mm	Ghigi (1921)	not indicated
	625 - 750 µm	Thiéry (1987)	Morocco
SPINICAUDATA			
Limnadia lenticularis	185 - 209 µm (n = 2)	This study	Slovakia
(V. I. = 12.18 %)	199 - 208 µm (n = 2)	This study	Slovakia
	200 - 208 µm	Thiéry & Gasc (1991)	not indicated
	0.15 - 0.22 mm	Lereboullet (1866)	not indicated
	0.15 - 0.17 mm	Zaffagnini (1967)	Italy
Imnadia yeyetta	180/180 - 185/190 µm (n = 2)	This study	Slovakia
(V. I. = 11.23 %)	165/150 - 175/160 µm (n = 6)	This study	France (Crau)
	185/182 µm	Thiéry & Gasc (1991)	not indicated
Cyzicus tetracerus	146 - 161 µm (n = 7)	This study	Slovakia
(V. I. = 14.30 %)	141 - 153 µm (n = 5)	This study	Slovakia
	145 - 150 µm	Thiéry & Gasc (1991)	France (Provence)
	139.5 µm	Alonso & Alcaraz (1984)	Spain
	0.15 - 0.16 mm	Mathias (1937)	France
Cyzicus grubei	124 µm	Alonso & Alcaraz (1984)	Spain
Cyzicus bucheti	150 - 190 µm	Thiéry (1987)	Morocco
Eocyzicus orientalis	119 - 122 µm (n = 2)	This study	Russia
(V. I. = 2.49 %)			
Leptestheria dahalacencis	95 - 103 µm (n = 3)	This study	Slovakia
(V. I. = 14.63 %)	103 - 110 µm (n = 8)	This study	Slovakia
	100 µm	Scanabissi Sabelli & Tommasini (1992)	Italy
Leptestheria mayeti	179 µm	Thiéry (1987)	Morocco
Eoleptestheria ticinensis	125 - 130 µm (n = 5)	This study	Slovakia
(V. I. = 6.35 %)	122 - 126 µm (n = 4)	This study	Slovakia
	127 µm	Thiéry & Gasc (1991)	France (Camargue)
LAEVICAUDATA			
Lynceus brachyurus	114 - 119 µm (n = 2)	This study	Slovakia
(V. I. = 4.29 %)			

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Three new species of *Hemicyclops* (Copepoda: Poecilostomatoida: Clausidiidae) from northwestern Madagascar

by Arthur G. HUMES

Abstract. — Three new species of the copepod genus *Hemicyclops* (Clausidiidae) from Nosy Bé, northwestern Madagascar, are described, from burrows of unknown origin, probably those of crustaceans, one from the scleractinian *Favia* sp., and one from a gastropod shell occupied by a hermit crab. *Hemicyclops acanthophorus*, new species, may be recognized by a pair of posterolateral spiniform processes on the genital double-somite of the female, and by the triangular form of the free segment of leg 5. *Hemicyclops apiculus*, new species, is characterized by its elongate genital double-somite with anterior rounded lateral expansions, its subquadrate caudal ramus, and the small sharply pointed lateral projections on the first segment of leg 5. *Hemicyclops vicinalis*, new species, may be distinguished by the absence of setules on the inner side of the caudal ramus and on the outer margin of the second segment of the antenna proximal to the seta.

Keywords. — Copepoda, Poecilostomatoida, Clausidiidae, *Hemicyclops*, Madagascar.

Trois nouvelles espèces d'*Hemicyclops* (Copepoda : Poecilostomatoida : Clausidiidae) du nord-ouest de Madagascar

Résumé. — Trois espèces nouvelles du genre *Hemicyclops* (Copepoda : Clausidiidae) de Nosy Bé, au nord-ouest de Madagascar, sont décrites, l'une provenant de terriers d'origine inconnue, probablement de crustacés, une autre provenant du scléractiniaire *Favia* sp., et la troisième d'une coquille de gastéropode occupée par un bernard-l'hermite. *Hemicyclops acanthophorus* n. sp. peut être identifiée par une paire de prolongements spiniformes postérolatéraux sur le somite génital de la femelle et la forme triangulaire du segment libre de la cinquième patte. *Hemicyclops apiculus* n. sp. se caractérise par un somite génital allongé avec des expansions latérales antérieures arrondies, des rames caudales subcarrées et la présence de petites projections pointues latérales sur le premier segment de la cinquième patte. *Hemicyclops vicinalis* n. sp. peut être identifiée par l'absence de sétules sur le bord interne de la rame caudale et au bord externe du deuxième segment de l'antenne.

Mots-clés. — Copépodes, Poecilostomatoida, Clausidiidae, *Hemicyclops*, Madagascar.

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INTRODUCTION

Since the revision of *Hemicyclops* by VERVOORT & RAMIREZ (1966), in which 23 valid species were recognized, several congeners have been described, extending the range of this clausidiid genus to Hong Kong (BOXSHALL & HUMES, 1987), Korea (HO & KIM, 1990, 1991; KIM & HO, 1992), Panama (HUMES, 1984), Curaçao (STOCK, 1992), Japan (ITOH & NISHIDA, 1993), and Brazil (KIHARA & DA ROCHA, 1994).

In addition to the species recognized in the work of VERVOORT & RAMIREZ (1966), the following species have been described : *Hemicyclops perinsignis* Humes, 1973, from the sponge *Agelas* sp. in Madagascar; *H. columnaris* Humes, 1984, from the scleractinian coral *Porites lobata*

Dana on the Pacific coast of Panama; *H. mortoni* Boxshall & Humes, 1987, from burrows of the echiuran *Ochetostoma erythrogrammon* Leuckhart & Rüppell at Hong Kong; *H. ctenidis* Ho & Kim, 1990, from the polychaete *Neanthes japonica* (Izuka) in Korea; *H. gomsoensis* Ho & Kim, 1991, from burrows occupied by the crab *Macrophthalmus japonicus* de Haan in Korea; *H. saxatilis* Ho & Kim, 1991, from burrows occupied by the crab *Heteropanope (Pilumnopeus) makinana* (Rathbun) in Korea; *H. geminatus* Stock, 1992, from the hermit crabs *Calcinus tibicen* (Herbst), *Paguristes grayi* Benedict, and *Dardanus venosus* (H. Milne Edwards) at Curaçao; *H. caissarum* Kihara & da Rocha, 1993, from burrows of the callianassid *Callichirus major* (Say) in Brazil; *H. japonicus* Itoh & Nishida, 1993, from dredged material in Tokyo Bay, Japan; and *H. sebastiani* Kihara & da Rocha, 1993, from the thalassinid *Callichirus guassutinga* (Rodriguez) in Brazil.

In this paper, three new species of *Hemicyclops*, all from northwestern Madagascar, are described. The number of valid species in the genus now stands at 36.

MATERIAL AND METHODS

The copepods from intertidal burrows were collected at low tide by means of a small bilge pump. In other cases, the host invertebrates were washed in a dilute solution of ethanol in sea water (approximately 5%) and the copepods recovered from the sediment obtained after passing the wash water through a fine net.

Lactic acid was used to clear the copepods for measurements and dissection. The length of the body does not include the setae on the caudal rami. The segments of the antennule were measured along their posterior nonsetiferous margins. In the formula for legs 1-4, Roman numerals indicate spines, Arabic numerals represent setae.

POECILOSTOMATOIDA Thorell, 1859
Family CLAUSIDIIDAE Embleton, 1901
HEMICYCLOPS Boeck, 1872

Hemicyclops acanthophorus n. sp.
(Figs 1-4)

TYPE MATERIAL. — 13 ♀♀, 5 ♂♂ from large burrows in intertidal sand, Befotaka, Nosy Bé, northwestern Madagascar, 29 April 1964. Holotype ♀ (MNHN – Cp 1052), allotype ♂ (MNHN – Cp 1053), and 12 paratypes (9 ♀♀, 3 ♂♂) (MNHN – Cp 1054) deposited in the Muséum national d'Histoire naturelle, Paris. Remaining paratypes (dissected) and copepodids (3 ♀♀, 1 ♂) in the collection of the author.

ETYMOLOGY. — The name of the species is formed from the Greek words *akantha*, a thorn or spine, and *phorein*, to bear or carry, alluding to the pair of small spiniform processes on the genital double-somite of the female.

DESCRIPTION OF FEMALE

Body (Fig. 1a) relatively slender. Length 1.35 mm (1.25-1.45 mm) and greatest width 0.56 mm (0.50-0.61 mm), based on 10 specimens. Greatest dorsoventral thickness 0.37 mm. Epimera of somites bearing legs 1-4 flaring outward and pointed. Somite bearing leg 1 fused

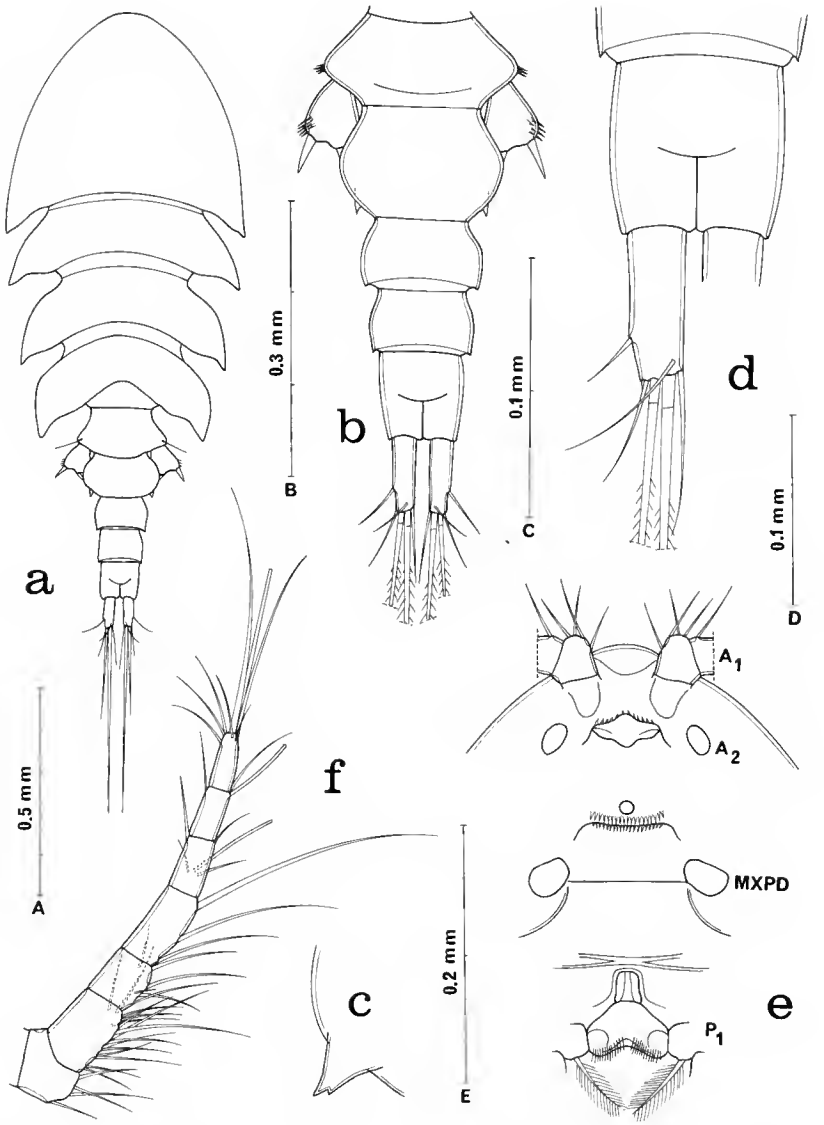

FIG. 1. — *Henicyclops acanthophorus*, n. sp., female. a, dorsal (scale A); b, urosome, dorsal (B); c, spiniform process on genital double-somite, lateral (C); d, anal somite and caudal ramus, dorsal (D); e, median part of cephalosome, showing rostrum, labrum, postoral area, and area between maxillipeds and first pair of legs, ventral (B); f, antennule, posteroventral (E). A_1 = antennule, A_2 = antenna, MXPD = maxilliped, P_1 = leg 1.

Hemicyclops acanthophorus, *n. sp., femelle. a, vue dorsale (échelle A); b, urosome, vue dorsale (B); c, processus spiniforme sur le double somite génital, vue latérale (C); d, somite anal et rames caudales, vue dorsale (D); e, partie médiane du céphalosome, montrant le rostre, le labre, la région postorale et la zone située entre les maxillipèdes et la première paire de pattes, vue ventrale (B); f, antennule, vue postéro-ventrale (E).* A_1 *= antennule,* A_2 *= antenne, MXPD = maxillipède,* P_1 *= première paire de pattes.*

with cephalosome. Ratio of length to width of prosome 1.66:1. Ratio of length of prosome to that of urosome 1.80: 1.

Somite bearing leg 5 (Fig. 1b) 101 × 218 µm. Genital double-somite 112 × 177 µm, wider than long, in dorsal view with gently rounded lateral margins and bearing pair of small posterolateral, unequally bifid, spiniform processes about 15 µm long (Fig. 1c), perhaps part of modified leg 6. Genital areas located laterally but no evidence of setae. Three postgenital somites 78 × 127, 75 × 103, and 88 × 86 µm.

Caudal ramus (Fig. 1d) unornamented, elongate, 75 × 26 µm, ratio 3: 1. Outer lateral seta 30 µm, dorsal seta 52 µm, outermost terminal seta 40 µm, innermost terminal seta 65 µm, all smooth. Two long median terminal setae 180 µm (outer) and 450 µm (inner), both with delicate short lateral setules.

Body surface without visible sensilla.

Egg sac not seen.

Rostrum (Fig. 1e) broadly rounded posteroventrally. Antennule (Fig. 1f) 308 µm long. Lengths of 7 segments : 13 (44 µm along anterior margin), 39, 36, 60, 39, 39, and 39 µm, respectively. Formula for armature: 4, 15, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth. Distal seta on segment 4 long, 250 µm.

Antenna (Fig. 2a) 4-segmented, with armature 1, 1, 4, and 7. First segment with long distal seta having lateral setules. Second segment with shorter smooth seta. Third segment with 3 slender setae, one of them with setules, and 1 swollen almost clawlike seta with recurved tip. Fourth segment with 6 smooth setae and 1 seta with setules.

Labrum (Fig. 1e) with marginal row of spines and pair of rows of small submarginal spines. Postoral area with 2 rows of spines (Fig. 2b).

Mandible (Fig. 2c) terminally with 2 stout elements and 2 setae. Paragnath (Fig. 2b) elongate lobe, 48 µm, with few minute setules. Maxillule (Fig. 2d) bearing 8 setae. Maxilla (Fig. 2e) with first segment bearing 2 long setae with setules and 1 very small setule; second segment with 3 setae and large bifurcate element. Maxilliped (Fig. 2f) 4-segmented, with 2 setae on first segment, 2 setae on second segment, and 6 setae on fourth segment, one of them slightly bent and having lateral setules.

Ventral area between maxillipeds and first pair of legs as in Fig. 1e.

Legs 1-4 (Figs 2g, h, 3a, b) segmented and armed as follows :

P_1	coxa 0-I	basis I-I	exp I-0; enp 0-1;	I-1; 0-I;	I,I,6 1,5
P_2	coxa 0-I	basis I-0	exp I-0; enp 0-1;	I-1; 0-2;	II,II,5 I,II,3
P_3	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	II,I,5 I,II,3
P_4	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	I,II,5 I,II,2

Intercoxal plate of leg 1 with slender setules on ventral margin; intercoxal plates of legs 2-4 with marginal spines.

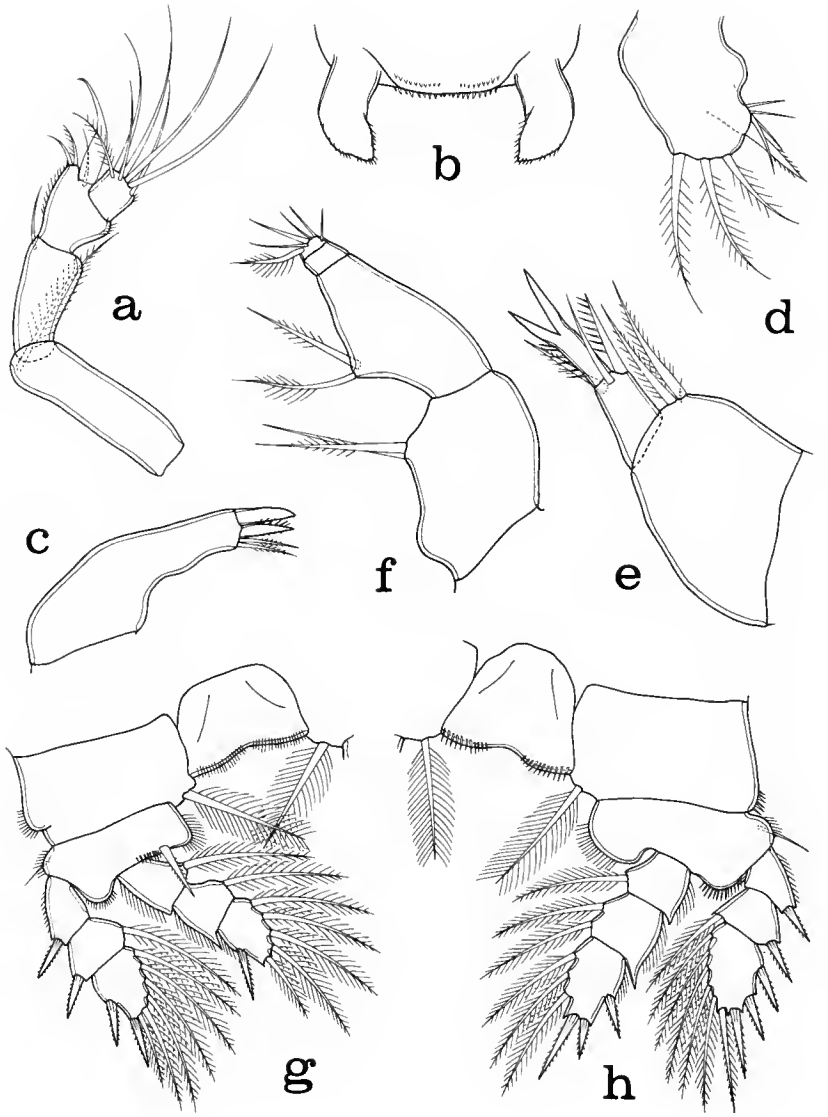

FIG. 2. — *Hemicyclops acanthophorus*, n. sp., female. a, antenna, posterior (scale D); b, postoral area and paragnaths, posterior (D); c, mandible, posterior (C); d, maxillule, posterior (C); e, maxilla, posterior (C); f, maxilliped, posterior (C); g, leg 1 and intercoxal plate, anterior (E); h, leg 2 and intercoxal plate, anterior (E).

Hemicyclops acanthophorus, *n. sp., femelle. a, antenne, face postérieure (échelle D); b, région postorale et paragnathes, vue postérieure (D); c, mandibule, vue postérieure (C); d, maxillule, vue postérieure (C); e, maxille, vue postérieure (C); f, maxillipède, vue postérieure (C); g, P_1 et plaque intercoxale, face antérieure (E); h, P_2 et plaque intercoxale, face antérieure (E).*

Leg 1 with inner spine on basis 50 µm. Other details of ornamentation as illustrated.

Leg 5 (Fig. 3c) with free segment triangular, 57 µm along inner side, 68 µm along outer side and 65 µm wide, armed with 3 spines and 1 small seta, these elements from outer to inner 47, 50, 22, and 42 µm. Segment ornamented near insertion of outermost seta with group of spinules. Dorsal seta 70 µm, with few spinules near its insertion.

Leg 6 not identified.

Living specimens in transmitted light opaque gray, eye red.

Description of male

Prosome slightly broader (Fig. 3d) than in female. Length 1.05 mm (1.00-1.08 mm) and greatest width 0.44 mm (0.43-0.46 mm), based on 5 specimens. Greatest dorsoventral thickness 0.28 mm. Internal sclerotizations visible along sides of prosome as in Fig. 3e. Somite bearing leg 4 having somewhat different form (Fig. 3d) than in female. Ratio of length to width of prosome 1.61:1. Ratio of length of prosome to that of urosome 1.40:1.

Segment bearing leg 5 (Fig. 4a) 70 x 153 µm. Genital somite 146 × 180 ×m, shape similar to that of female, but lacking pair of spiniform processes. Four postgenital somites 65 × 112, 60 × 91, 40 × 81, and 42 × 74 µm.

Caudal ramus like that of female but smaller, 61 × 25 µm.

Body surface unornamented.

Rostrum similar to that of female. Antennule like that of female, but extra seta added on segments 3 and 4. Antenna like that of female.

Labrum, mandible, paragnath, maxillule, and maxilla resembling those of female. Maxilliped (Fig. 4b, c) with long seta on first segment. Second segment expanded, with 2 inner setae and 2 rows of spines, those in one row stout, those in other row slender. Claw 148 µm long with slight protuberance on concave margin, and bearing 2 small proximal setae.

Postoral area as in female.

Leg 1 (Fig. 4d) lacking inner spine on basis (as in many congeners), but otherwise as in female. Legs 2-4 like those of female.

Leg 5 (Fig. 4e) with free segment elongate, 91 × 47 µm, ornamented with spinules along both sides; armature as in female.

Leg 6 (Fig. 4f) consisting of posteroventral flap on genital somite bearing 1 seta 26 µm.

Spermatophore not seen.

Color as in female.

Remarks

Hemicyclops acanthophorus may be distinguished from all other species in the genus by the presence of a pair of small thornlike posterolateral spiniform processes on the genital double-somite of the female. The triangular shape of the free segment of leg 5 in the female is also characteristic.

Although the occupants of the burrows in which the copepods were found is not known, it is likely that they were crustaceans. Several species of *Hemicyclops* are known from burrows of crustaceans at Nosy Bé, Madagascar: *H. axiophilus* Humes, 1965, and *H. amplicaudatus*

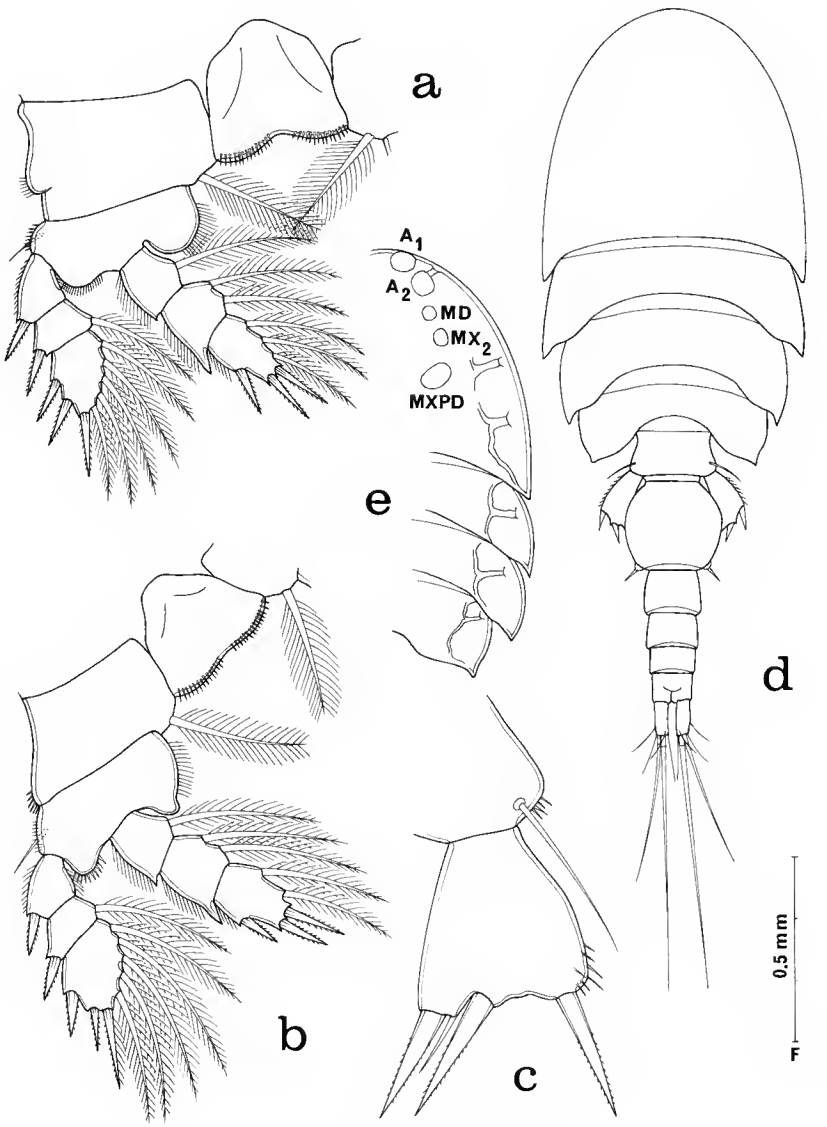

FIG. 3. — *Hemicyclops acanthophorus*, n. sp., female. a, leg 3 and intercoxal plate, anterior (scale E); b, leg 4 and intercoxal plate, anterior (E); c, leg 5, dorsal (C). Male. d, dorsal (F); e, side of prosome showing internal sclerotizations, dorsal (F). A_1 = antennule, A_2 = antenna, MD = mandible, MX_2 = maxilla, MXPD = maxilliped.

Hemicyclops acanthophorus, *n. sp., femelle. a, P3 et plaque intercoxale, face antérieure (échelle E); b, P4 et plaque intercoxale, face antérieure (E); c, P5, vue dorsale (C). Mâle. d, vue dorsale (F); e, bord du prosome montrant des sclérotisations internes, vue dorsale (F).* A_1 *= antennule,* A_2 *= antenne, MD = mandibule,* MX_2 *= maxille; MXPD = maxillipède.*

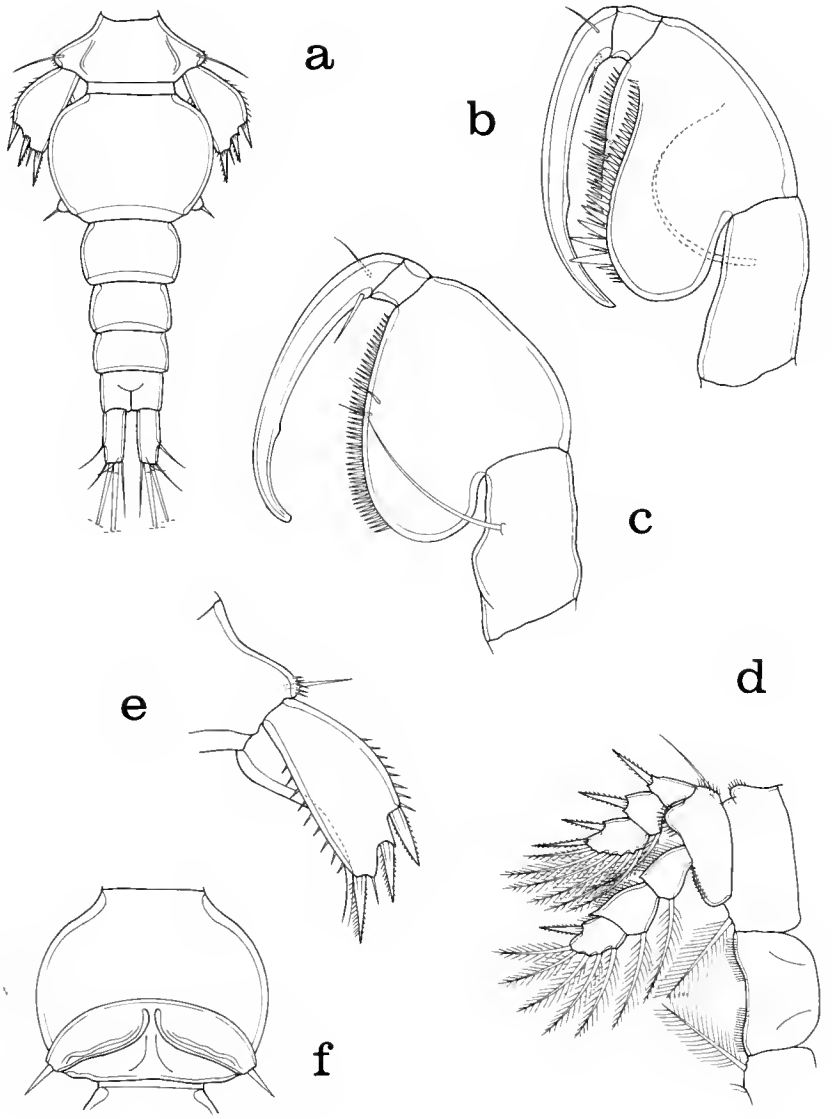

FIG. 4. — *Hemicyclops acanthophorus*, n. sp., male. a, urosome, dorsal (scale B); b, maxilliped, posterior (D); c, maxilliped, anterior (D); d, leg 1 and intercoxal plate, anterior (E); e, leg 5, ventral (D); f, genital somite, ventral (E).

Hemicyclops acanthophorus, *n. sp., mâle. a, urosome, vue dorsale (échelle B); b, maxillipède, vue postérieure (D); c, maxillipède, vue antérieure (D); d, P_1 et plaque intercoxale, vue antérieure (E); e, P_5, vue ventrale (D); f, somite génital, face ventrale (E).*

Humes, 1965, from burrows of the thalassinidean macruran *Axius (Neaxius) acanthus* (Axiidae); *H. acanthosquillae* Humes, 1965, from the body of the stomatopod *Acanthosquilla* sp. (= *A. humesi* Manning) dug from intertidal sand; and *H visendus* Humes, Cressey, and Gooding, 1958, from the body surface of the thalassinidean macruran *Upogebia (Upogebia)* sp. (Callianassidae) in burrows (Humes, 1965).

Hemicyclops apiculus n. sp.

(Figs 5-7)

TYPE MATERIAL. — 3 ♀♀ from washing of one colony of the scleractinian coral *Favia* sp., in 3 m, Pointe-à-la-Fièvre, Nosy Bé, northwestern Madagascar, 26 December 1963. Holotype (MNHN – Cp 1055) and 1 paratype (MNHN – Cp 1056) deposited in the Muséum national d'Histoire naturelle, Paris. Remaining paratype (dissected) in the collection of the author.

OTHER SPECIMEN. — 1 ♀ from the ahermatypic coral *Dendrophyllia* sp., in 7 m, Nosy Tangam, near Nosy Bé, 1 January 1964.

ETYMOLOGY. — The specific name *apiculus*, Latin meaning "pointed", alludes to the small sharp projection on the first segment of leg 5.

DESCRIPTION OF FEMALE

Body (Fig. 5a, b) moderately slender. Length 1.42 mm (1.36-1.50 mm) and greatest width 0.51 mm (0.48-0.54 mm), based on 3 specimens. Greatest dorsoventral thickness 0.33 mm. Somite bearing leg 1 fused with cephalosome. Epimera of somites bearing legs 1-4 pointed posteriorly in somites bearing legs 1 and 2, less pointed in somites bearing legs 3 and 4. Ratio of length to width of prosome 1.58:1. Ratio of length of prosome to that of urosome 1.22:1.

Somite bearing leg 5 (Fig. 5c) 109 × 268 µm. Genital double-somite in dorsal view much longer than wide, 273 µm long, 213 µm wide in expanded anterior third, and 122 µm wide in posterior two-thirds with parallel sides. Posterolateral corners of anterior expanded portion bluntly produced. Ratio of length to greatest width 1.28:1. Genital openings situated laterally (Fig. 5b) and lacking setae but showing 2 minute knoblike projections. Three postgenital somites from anterior to posterior 107 × 130, 78 × 122, and 65 × 120 µm.

Caudal ramus (Fig. 6a) subquadrate, 65 × 60 µm, only slightly longer than wide. Outer lateral seta 44 µm, dorsal seta 88 µm, both smooth. Outermost terminal seta 96 µm, innermost terminal seta 208 µm, and 2 long median terminal setae 360 µm (outer) and 580 µm (inner), all with lateral setules, those on 2 median setae long and placed well apart. Postero-inner corner of ramus with small spiniform projection 5 µm long.

Body surface without visible ornamentation.

Egg sac not seen.

Rostrum (Fig. 6b) triangular and bluntly pointed posteroventrally. Antennule (Fig. 6c) 385 µm long. Lengths of its 7 segments: 17 (52 µm along anterior margin), 47, 31, 90, 60, 44, and 52 µm, respectively. Formula for armature: 4, 15, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth.

Antenna (Fig. 6d) 4-segmented with formula 1, 1, 3 + 1 spine, and 7. Second segment with setules on both sides, third segment with outer setules, and fourth segment with inner setules. Seta on segment 1 with bilateral setules. Seta on segment 2 with long unilateral setules. One

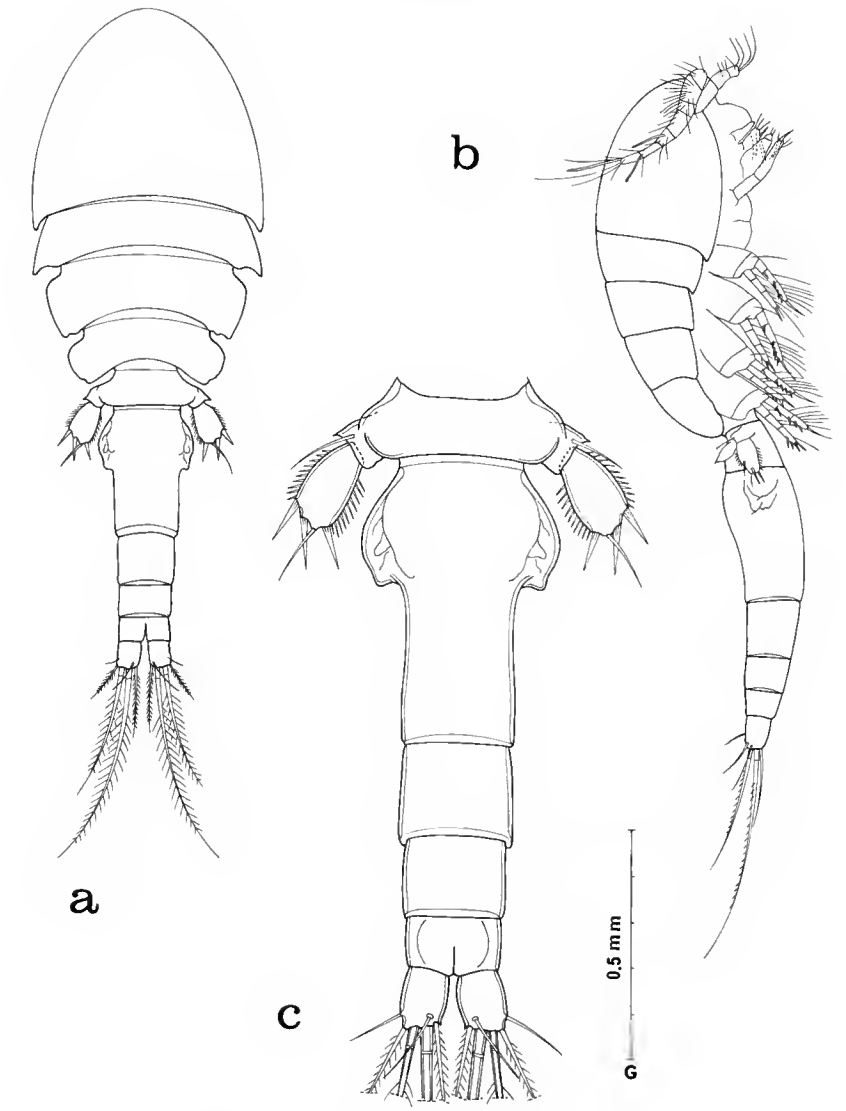

FIG. 5. — *Hemicyclops apiculus*, n. sp., female. a, dorsal (scale G); b, lateral (G); c, urosome, dorsal (B).
Hemicyclops apiculus, *n. sp., femelle. a, vue dorsale (échelle G); b, vue latérale (G); c, urosome, vue dorsale (B).*

seta on segment 3 with several unilateral spinules, other setae and spine smooth. One seta on segment 4 with long spinules, other 6 setae smooth, 4 longest of these slightly geniculate.

Labrum (Fig. 6b) with row of short spinules anteriorly, followed by row of small blunt spinules; another interrupted row of small setae posteriorly. Postoral area (Fig. 6e) with 6 submarginal spines and row of minute marginal spinules; corners of labium with prominent tooth.

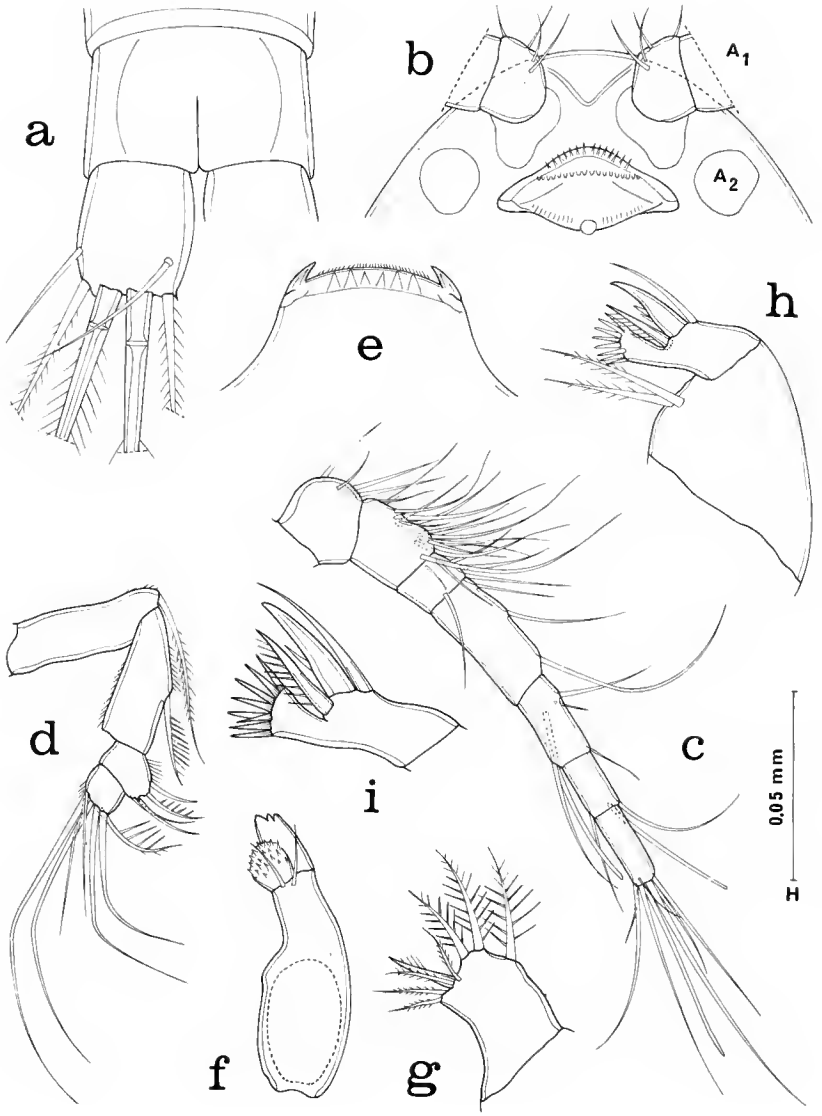

FIG. 6. — *Hemicyclops apiculus*, n. sp., female. a, anal somite and caudal ramus, dorsal (scale D); b, rostrum and labrum, ventral (E); c, antennule, ventral (E); d, antenna, anterior (E); e, postoral area, ventral (H); f, mandible, anterior (D); g, maxillule, anterior (D); h, maxilla, anterior (D); i, second segment of maxilla, posterior (C). A_1 = antennule, A_2 = antenna.

Hemicyclops apiculus, *n. sp., femelle. a, somite anal et rames caudales, vue dorsale (échelle D); b, rostre et labre, vue ventrale (E); c, antennule, face ventrale (E); d, antenne, face antérieure (E); e, région postorale, vue ventrale (H); f, mandibule, vue antérieure (D); g, maxillule, vue antérieure (D); h, maxille, vue antérieure (D); i, deuxième segment de la maxille, face postérieure (C).* A_1 *= antennule,* A_2 *= antenne.*

Mandible (Fig. 6f) terminally with 2 stout elements, one dentate, other spinulose, and 2 setae. Maxillule (Fig. 6g) bearing 8 setae, in groups of 5 + 3. Maxilla (Fig. 6h) with first segment bearing 2 long setae. Second segment (Fig. 6i) bearing 1 smooth seta, clawlike spine bearing 1 inner spinule, and 1 spiniform seta with unilateral setules; segment with prolongation bearing terminal row of 8 smooth spines. Maxilliped (Fig. 7a) with 2 setae on both first and second segments. Small third segment unarmed. Minute fourth segment with 2 unequal clawlike spines 62 µm and 42 µm, and 3 slender setae.

Ventral area between maxillipeds and first pair of legs slightly protuberant (Fig. 5b) and appearing as in Fig. 7b.

Legs 1-4 (Fig. 7c-f) with 3-segmented rami armed as follows:

P_1	coxa 0-1	basis 1-I	exp I-0; enp 0-1;	I-1; 0-1;	II,6 I,5
P_2	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-I; 0-2;	III,I,5 I,II,3
P_3	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	III,I,5 II,II,2
P_4	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	II,I,5 II,II,I

Intercoxal plate of leg 1 with slender setules on ventral margin; intercoxal plates of legs 2-4 with marginal spines.

Basis of leg 1 with inner spine 50 µm. Exopod of leg 1 with 2 distal spines on third segment setiform, with small spinules along outer margin and setules along inner margin; innermost seta on third segment of endopod slender, short, and smooth. Distal spine on third segment of exopod in legs 2-4 setiform.

Leg 5 (Fig. 7g) 2-segmented, with free segment in dorsal view 99 × 55 µm, in flat view 94 × 60 µm (as in Fig. 7h). Four terminal elements (3 spines and 1 seta) from outer to inner 39, 45, 65, and 58 µm. Both sides of free segment with prominent setules. First segment, fused with body somite, having pointed outer projection and bearing dorsal seta 60 µm.

Leg 6 not identified but possibly represented by 2 minute knobs (Fig. 5b).

Color of living specimens in transmitted light slightly yellow, eye red, ovaries lemon yellow.

Male unknown.

Remarks

Among the many species of *Hemicyclops*, seven have an elongate genital double-somite with rounded anterior expansions, as in the new species. *Hemicyclops apiculus*, new species, may be distinguished from the female of all seven of these congeners in the following ways. In *H. kombensis* Humes, 1965, and *H. acanthosquillae* Humes, 1965, the body is more than 2 mm in length. In *H. biflagellatus* Humes, 1965, the body length is more than 2 mm and the somite bearing leg 5 has a pair of setiform processes (setae?). In *H. columnaris* Humes, 1984, the body is smaller (average length 1.13 mm) and the ratio of length to width of the caudal ramus is

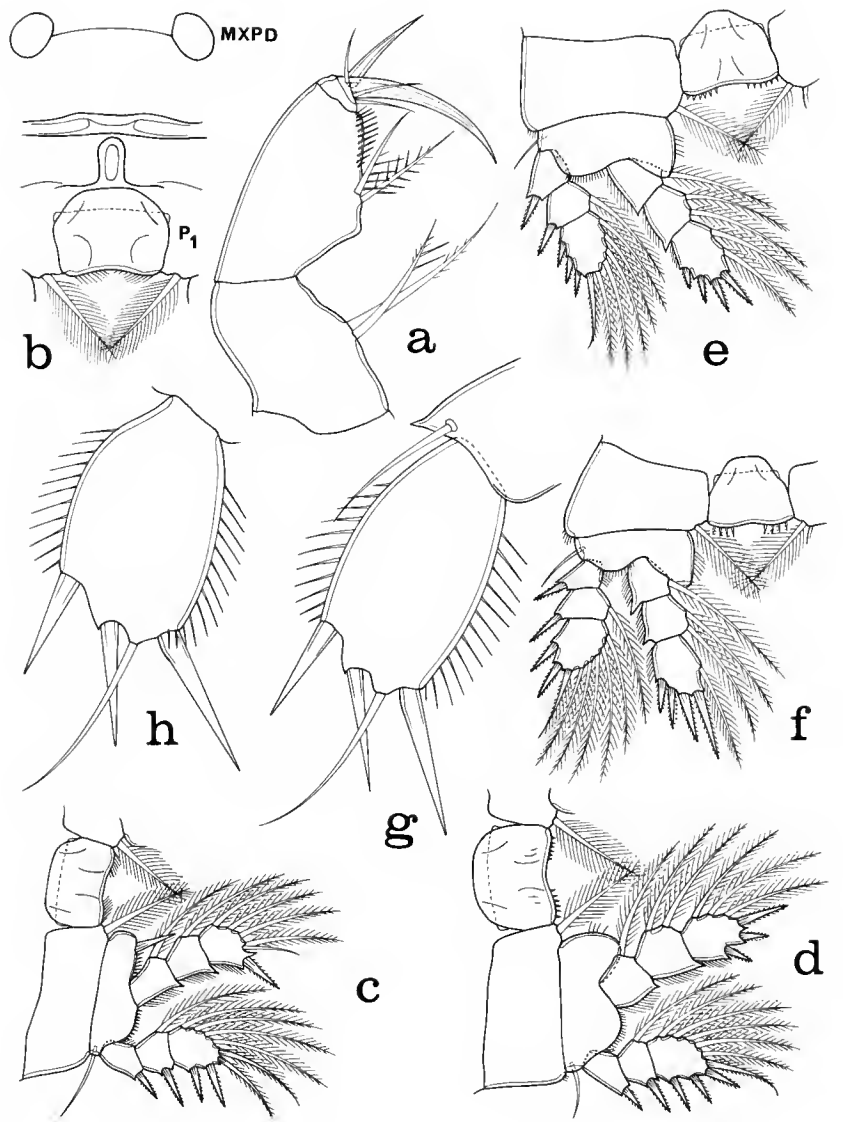

FIG. 7. — *Hemicyclops apiculus*, n. sp., female. a, maxilliped, posterior (scale D); b, area between maxillipeds and first pair of legs, ventral (E); c, leg 1 and intercoxal plate, anterior (B); d, leg 2, and intercoxal plate, anterior (B); e, leg 3 and intercoxal plate, anterior (B); f, leg 4 and intercoxal plate, anterior (B); g, leg 5, dorsal (C); h, second segment of leg 5, flat ventral view (C). MXPD = maxilliped, P_1 = leg 1.

Hemicyclops apiculus, *n. sp., femelle. a, maxillipède, vue postérieure (échelle D); b, zone située entre les maxillipèdes et la première paire de pattes, face ventrale (E); c, P_1 et plaque intercoxale, face antérieure (B); d, P_2 et plaque intercoxale, face antérieure (B); e, P_3 et plaque intercoxale, vue antérieure (B); f, P_4 et plaque intercoxale, face antérieure (B); g, P_5, vue dorsale (C); h, deuxième segment de P_5, vue ventrale (C). MXPD = maxillipède, P_1 = première paire de pattes.*

1.7:1. In *H. perinsignis* Humes, 1973, the free segment of leg 5 is short and broad, ratio 1.5:1, and the ratio of the caudal ramus is 1.72:1. In *H. saxatilis* Ho & Kim, 1991, the body length is about 2:1, and the genital double-somite has 2 pointed leaflike extensions laterally. *Hemicyclops australis* Nicholls, 1944, is poorly known, but may be distinguished by the posterolateral projections on the swollen portion of the genital double-somite.

Hemicyclops vicinalis n. sp.
(Figs 8-11)

TYPE MATERIAL. — 2 ♀♀, 1 ♂ from one hermit crab, *Dardanus guttatus* (Olivier), in shell of *Conus* sp., 1.5 m, Ankify, near Nosy Bé, Madagascar, 48°20'15"E, 13°30'30"S, 30 December 1963. Holotype ♀ (MNHN – Cp 1057) and allotype ♂ (dissected) (MNHN – Cp 1058) deposited in the Muséum national d'Histoire naturelle, Paris. One paratype ♀ (dissected) in the collection of the author.

ETYMOLOGY. — The specific name *vicinalis*, Latin meaning "neighboring" or "near", alludes to the close similarity in external anatomy to *H. columnaris* and *H. geminatus* Stock, 1992.

DESCRIPTION OF FEMALE

Body (Fig. 8a, b) with moderately broad prosome. Length 1.16 mm (1.08-1.23 mm) and greatest width 0.44 mm (0.42-0.46 mm), based on 2 specimens. Greatest dorsoventral thickness 0.31 mm. Somite bearing leg 1 not separated dorsally from cephalosome. Epimera of metasomal somites rounded except pointed on somite bearing leg 1. Ratio of length to width of prosome 1.26:1. Ratio of length of prosome to that of urosome 1.11:1.

Somite bearing leg 1 (Fig. 8c) 109 × 218 µm. Genital double-somite elongate, cylindrical, in dorsal view 239 µm long, 185 µm wide at small lateral swellings in anterior third, and 156 µm wide posteriorly. Ratio of length to greatest width 1.77:1. Genital openings, lacking setae or spines, situated laterally at level of lateral swellings. Three postgenital somites from anterior to posterior 88 × 133, 55 × 120, and 52 × 109 µm. Anal somite with posteroventral row of spines on its distal edge (Fig. 8d).

Caudal ramus (Fig. 8d) subquadrate, little wider proximally than distally, length 61 µm, proximal width 50 µm, distal width 44 µm. Ratio (taking width at middle) 1.17:1. Outer lateral seta 47 µm and dorsal seta 95 µm, both smooth. Outermost terminal seta 96 µm, innermost terminal seta 170 µm, both with small lateral setules. Two median terminal setae in holotype: outer 350 µm with lateral setules, inner broken at proximal joint. Inner distal corner of ramus with minute setule 3 µm long.

Body surface lacking visible ornamentation.

Egg sac (Fig. 8e) elongate, 440 × 132 µm, with many eggs, each with diameter of approximately 42 µm.

Rostrum (Fig. 8f) broadly rounded. Antennule (Fig. 9a) 320 µm long, lengths of its 7 segments: 13 (44 µm along anterior margin), 37, 34, 55, 39, 44, and 42 µm, respectively. Armature: 4, 15, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth. Antenna (Fig. 8b) 4-segmented, with armature 1, 1, 4, and 7. Seta on second segment relatively short and weak. Otherwise similar to *Hemicyclops acanthophorus*, new species, except for minor setation.

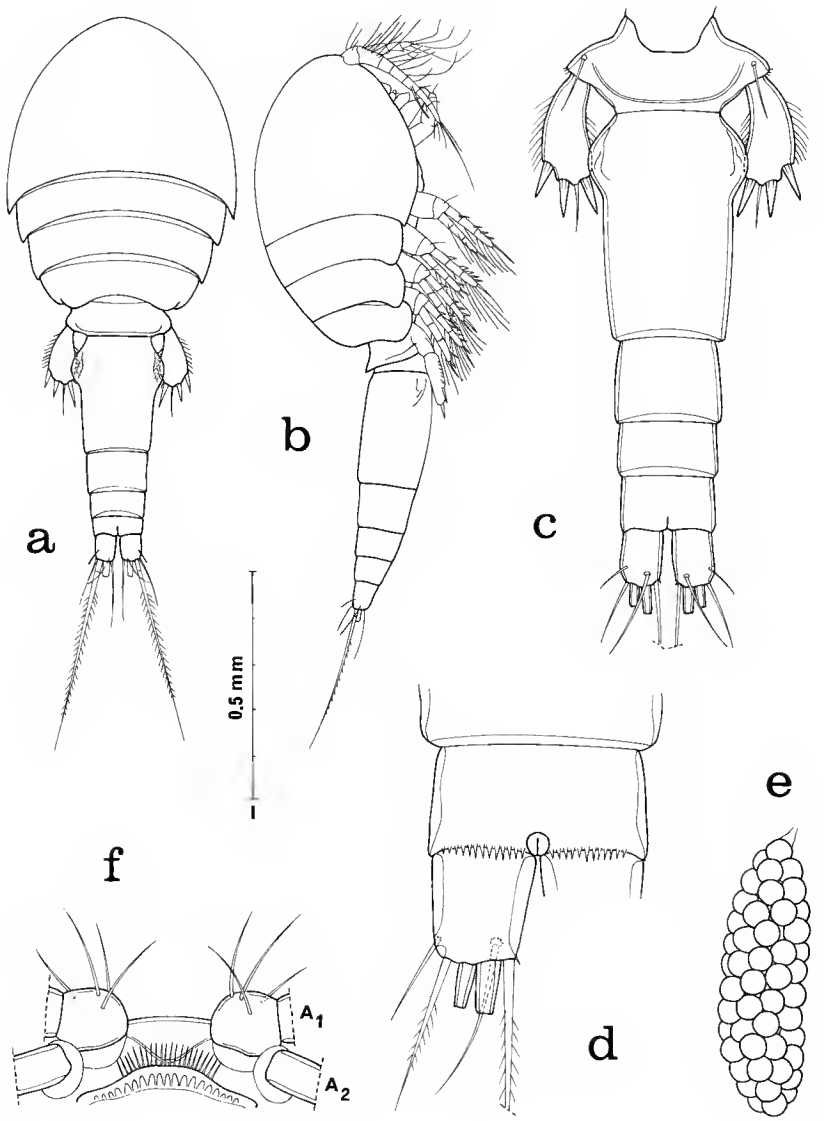

FIG. 8. — *Hemicyclops vicinalis*, n. sp., female. a, dorsal (scale 1); b, lateral (I); c, urosome, dorsal (B); d, anal somite and caudal ramus, dorsal (D); e, egg sac, ventral (A); f, rostrum and edge of labrum, ventral (D). A_1 = antennule, A_2 = antenna.

Hemicyclops vicinalis, *n. sp., femelle. a, vue dorsale (échelle I); b, vue latérale (I); c, urosome, vue dorsale (B); d, somite anal et rames caudales, vue dorsale (D); e, sac ovigère, vue ventrale (A); f, rostre et bord du labre, vue ventrale (D).* A_1 *= antennule,* A_2 *= antenne.*

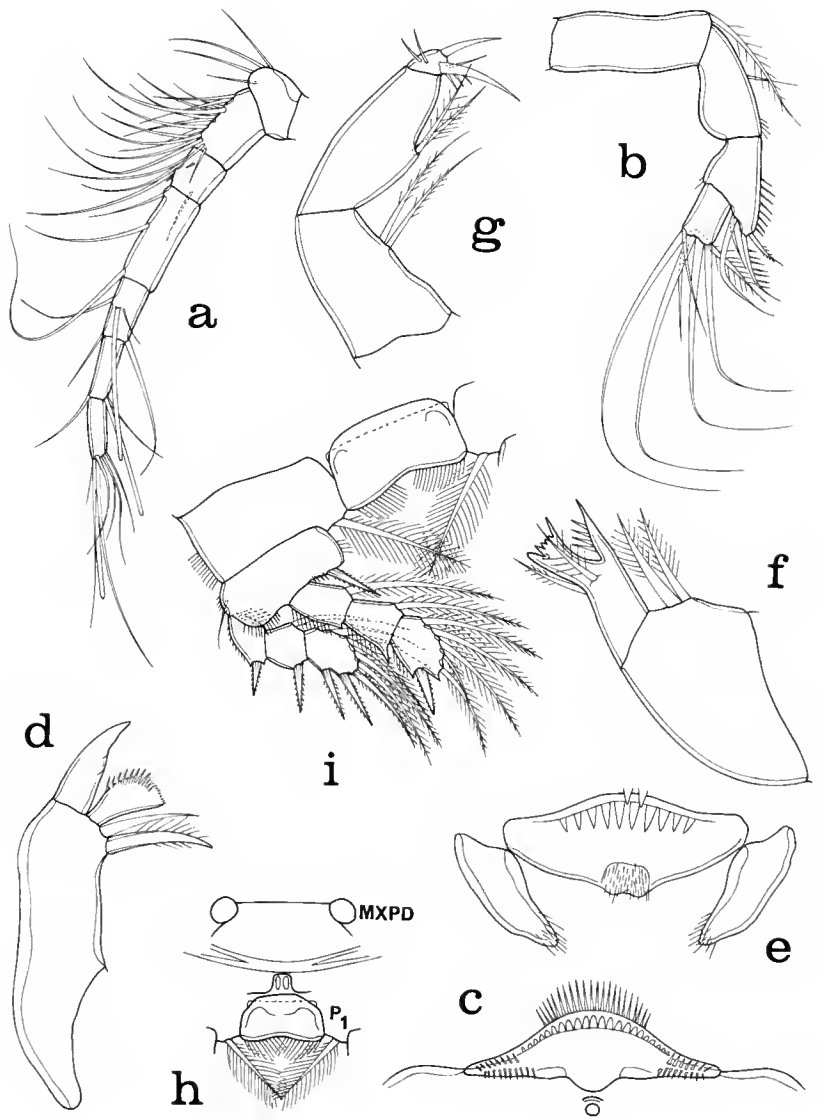

FIG. 9. — *Hemicyclops vicinalis*, n. sp., female. a, antennule, dorsal (scale E); b, antenna, anterior (D); c, labrum, ventral (C); d, mandible, posteroventral (C); e, postoral area and paragnaths, ventral (C); f, maxilla, posterior (D); g, maxilliped, posterior (D); h, area between maxillipeds and first pair of legs, ventral (B); i, leg 1 and intercoxal plate, anterior (E). MXPD = maxilliped, P_1 = leg 1.

Hemicyclops vicinalis, *n. sp., femelle. a, antennule, face dorsale (échelle E); b, antenne, face antérieure (D); c, labre, face ventrale (C); d, mandibule, vue postéro-ventrale (C); e, région post-orale et paragnathes, vue ventrale (C); f, maxille, face postérieure (D); g, maxillipède, vue postérieure (D); h, zone située entre les maxillipèdes et la première paire de pattes, vue ventrale (B); i, P_1 et plaque intercoxale, face antérieure (E). MXPD = maxillipède, P_1 = première paire de pattes.*

Labrum (Fig. 9c) with anterior row of long setae and subanterior row of blunt hyaline spines, and having 2 rows of setules at each side. Postoral area (Fig. 9e) with row of hyaline spines and median finely setulose area. Mandible (Fig. 9d) with stout elongate nonsetulose element, spatulate element with marginal setules, and 2 slender setae, one spiniform with lateral setules. Paragnath (Fig. 9e) attenuated lobe with distal hairlike setules. Maxillule as in Fig. 11c of male. Maxilla (Fig. 9f) and maxilliped (Fig. 9g) as illustrated

Ventral area between maxillipeds and first pair of legs protruding slightly (Fig. 8b). Two small sclerites in front of intercoxal plate of leg 1 (Fig. 9h).

Legs 1-4 (Figs 9i, 10a-c) with segmentation and armature as follows:

P_1	coxa 0-1	basis 1-I	exp I-0; enp 0-1;	I-1; 0-1;	II,6 I,5
P_2	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	III,I,5 I,II,3
P_3	coxa 0-I	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	III,I,5 I,II,3
P_4	coxa 0-1	basis 1-0	exp I-0; enp 0-1;	I-1; 0-2;	II,II,5 I,II,2

Intercoxal plate of leg 1 with slender setules along ventral edge; intercoxal plates of legs 2-4 with marginal spines.

In leg 1 inner spine on basis 49 µm long. In all 4 legs distal spine on third segment of exopod setiform, and outer margin of coxa and basis with setules. Other setules and spinules resembling those in other species, for example, *Hemicyclops columnaris* Humes, 1984.

Leg 5 (Fig. 10d) 2-segmented. First segment with dorsal seta 50 µm long. Second segment elongate, narrow proximally, widened distally, 117 × 50 µm (greatest width). Ratio 2.34:1. Terminally with 3 spines and 1 seta, from outer to inner 44, 36, 62, and 52 µm. Innermost spine with setules along inner margin. Seta reaching only to middle of genital double-somite. Both outer and inner margins of second segment with strong setules.

Leg 6 not identified.

Living specimens in transmitted light nearly translucid, eye red, egg sacs dull orange brown.

Description of male

Body (Figs 10e, 11a) resembling in general form that of female. Length (of allotype) 1.25 mm and width 0.45 mm. Greatest dorsoventral thickness 0.26 mm. Ratio of length to width of prosome 1.57:1. Ratio of length of prosome to that of urosome 1.24:1.

Somite bearing leg 5 (Fig. 11b) 91 × 198 µm. Genital somite subquadrate, 146 × 156 µm, slightly wider than long. Four postgenital somites from anterior to posterior 112 × 133, 88 × 122, 60 × 114, and 48 × 104 µm. Anal somite with posteroventral spinules as in female.

Caudal ramus like that of female.

Body surface lacking visible ornamentation.

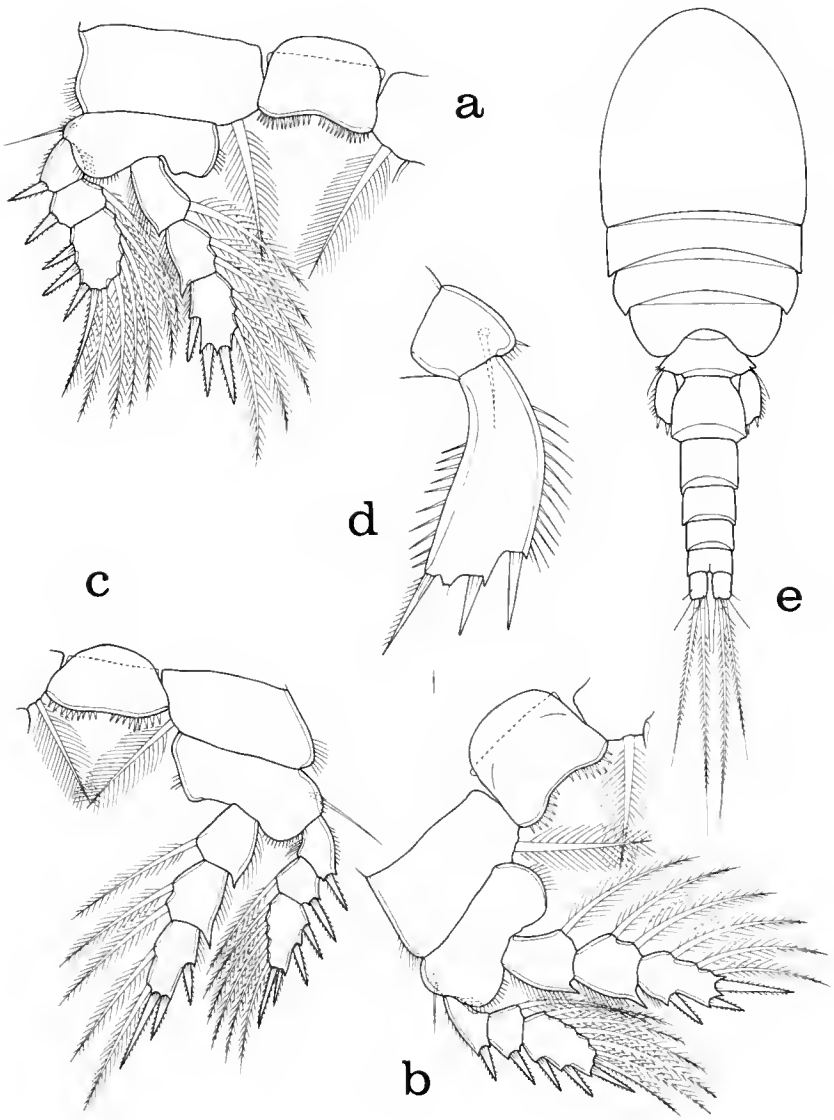

FIG. 10. — *Hemicyclops vicinalis*, n. sp., female. a, leg 2 and intercoxal plate, anterior (scale E); b, leg 3 and intercoxal plate, anterior (E); c, leg 4 and intercoxal plate, anterior (E); d, leg 5, ventral (D). Male. e, dorsal (I).

Hemicyclops vicinalis, *n. sp., femelle. a, P_2 et plaque intercoxale, face antérieure (échelle E) ; b, P_3 et plaque intercoxale, face antérieure (E) ; c, P_4 et plaque intercoxale, face antérieure (E) ; d, P_5, vue ventrale (D). Mâle. e, vue dorsale (I).*

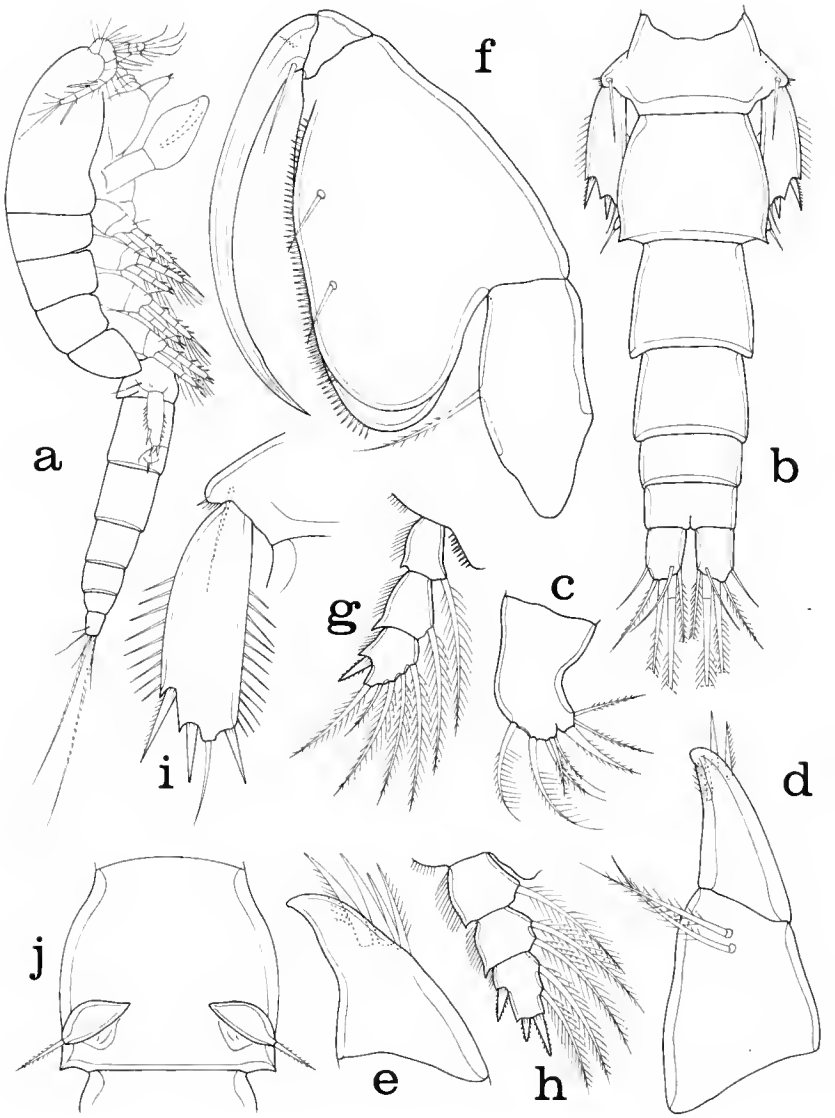

FIG. 11. — *Hemicyclops vicinalis*, n. sp., male. a, lateral (scale I); b, urosome, dorsal (B); c, maxillule, antero-inner (D); d, maxilla, anterior (D); e, second segment of maxilla, anterior (C); f, maxilliped, anterior (D); g, endopod of leg 1, anterior (E); h, endopod of leg 2, anterior (E); i, leg 5, ventral (D); j, genital somite showing sixth pair of legs (E).

Hemicyclops vicinalis, *n. sp., mâle. a. vue latérale (échelle I); b, urosome, vue dorsale (B); c, maxillule, vue antéro-interne (D); d, maxille, face antérieure (D); e, deuxième segment de la maxille, face antérieure (C); f, maxillipède, vue antérieure (D); g, endopodite de* P_1*, face antérieure (E); h, endopodite de* P_2*, face antérieure (E); i,* P_5*, vue ventrale (D); j, somite génital montrant la sixième paire de pattes (E).*

Rostrum as in female. Antennule similar to female but 1 seta added on segment 3 and another seta on segment 4. Antenna like that of female. Labrum, postoral area, mandible, paragnath, and maxillule (Fig. 11c) resembling those of female. Maxilla (Fig. 11d) with 2 setae on segment 1; segment 2 stoutly pointed and bearing 4 setae (Fig. 11e). Maxilliped (Fig. 11f) similar to that of *H. columnaris*.

Legs 1-4 with segmentation and armature as in female, but basis of leg 1 lacking inner spine seen in female (Fig. 1g). Segments of endopod of leg 2 (Fig. 11h) somewhat shorter than in female.

Leg 5 (Fig. 11i) with second segment 127 × 49 µm. Ratio 2.59:1. Less tapered than in female but otherwise similar.

Leg 6 (Fig. 11j) consisting of posteroventral flap on genital segment bearing 1 finely barbed spinelike seta 36 µm.

Spermatophore not seen.

Color as in female.

Remarks

Three species of *Hemicyclops*, *H. columnaris* from Pacific Panama, *H. geminatus* from Curaçao, and *H. vicinalis* from Madagascar, are at first glance remarkably similar. All have, in the female, an elongate columnar genital double-somite with small rounded anterior lateral expansions and a short caudal ramus with a length to width ratio less than 2:1. However, there are subtle differences that separate them and in particular distinguish the new species. In *H. vicinalis*, the inner margin of the caudal ramus is smooth (in *H. columnaris* and *H. geminatus* this margin bears setules); the length to width ratio of the caudal ramus in the female is 1.17:1 (1.7:1 in H. columnaris, 1.27-1.52:1 in *H. geminatus*); the outer side of segment 2 of the antenna proximal to the seta lacks setules (these setules present in *H. columnaris* and *H. geminatus*); the second segment of leg 5 is 117 × 50 µm (125 × 57 µm in *H. columnaris*, 85 × 40 µm in *H. geminatus*); and the inner of the two stout elements on the mandible is tapered proximally and is expanded and rounded distally (in *H. columnaris* this element is not tapered proximally and is rounded distally, in *H. geminatus* it is not tapered proximally and has a truncate tip). In *H. columnaris* the outermost terminal seta on the caudal ramus has a small thornlike process on its outer edge, not found in the two congeners mentioned. In *H. geminatus* the seta on the second segment of leg 5 in the female is much longer than in *H. vicinalis*, "reaching to 75-90% of length of genital segment" (Stock, 1992).

In all three species discussed, there are ventrodistal spinules on the anal somite (these not mentioned in the original description of *H. columnaris*).

Notes on **Hemicyclops perinsignis** Humes, 1973

This species, described from specimens associated with the sponge *Agelas*, has now been found associated with the alcyonacean coral *Tubipora musica* L. as follows: 5 ♀♀, 1 ♂ from 1 colony, Pointe Lokobe, Nosy Bé, Madagascar, 5 June 1967; 2 ♀♀, 1 ♂ from 1 colony, same locality, 12 June 1967.

Acknowledgements

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Barnacles (Cirripedia: Thoracica) of seas off the Straits of Gibraltar

by Brian A. FOSTER[1] and John S. BUCKERIDGE

Abstract. — The barnacles collected in dredges and grabs from stations in and off the Straits of Gibraltar (BALGIM 1984 cruise) which were sorted at CENTOB in Brest, are systematically considered. A few other deep-sea barnacles are also considered. Of the eighteen species illustrated, three are new to science. Particular attention is given to species of Scalpellinae with eleven species (two new), and Verrucidae with four species (one new). This paper determines only the species and their biogeography, leaving aside questions of generic categorisation, phylogeny, and the particular ecological and hydrological circumstances of each cruise.

Keywords. — Gibraltar, Poecilasmatidae, Scalpellidae, Verrucidae, Pachylasmatidae, Balanidae, new taxa, biogeography.

Cirripèdes (Cirripedia, Thoracica) récoltés dans les eaux du détroit de Gibraltar

Résumé. — Les Cirripèdes récoltés, principalement à l'aide de dragues et de bennes, au voisinage et dans le détroit de Gibraltar lors de la campagne BALGIM, sont étudiés ici d'un point de vue systématique. Quelques autres Cirripèdes de mer profonde sont également examinés. Tout le matériel étudié a été trié au CENTOB à Brest. Au total dix-huit espèces sont recensées et figurées, trois d'entre elles sont nouvelles pour la science. Une attention particulière est portée aux espèces des sous-familles Scalpellinae, au nombre de onze dont deux nouvelles, et Verrucidae, au nombre de quatre dont une nouvelle. Dans ce travail, nous n'avons considéré que l'identification des espèces et leur biogéographie. Les problèmes posés par les genres et la phylogénie, ainsi que les conditions hydrologiques et les particularités écologiques propres à chaque campagne n'ont pas été abordés.

Mots-clés. — Gibraltar, Poecilasmatidae, Scalpellidae, Verrucidae, Pachylasmatidae, Balanidae, espèces nouvelles, biogéographie.

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INTRODUCTION

This paper reports on a collection of barnacles the late Professor Brian FOSTER received from the Centre national de tri d'océanographie biologique (CENTOB), Brest. They were collected by the BALGIM expedition, during May-June 1984, from either side of the Straits of Gibraltar, particularly into the Ibero-Moroccan Bay of the Atlantic Ocean, by R. V. "Cryos" on behalf of the Centre national de la recherche scientifique (PIROCEAN) under the direction of Dr P. BOUCHET. Eighteen different species of cirripedes, from 126 stations were collected. A further ten samples from various deep-sea cruises in the Atlantic Ocean and three samples from the CORINDON II cruise in Indonesia were also forwarded for determination and contained specimens useful for present purposes. All stations and species data are listed in Appendix A.

1. Deceased, formerly of the Zoology Department, University of Auckland, Auckland, New Zealand.

The main collection results primarily from multiple deep-sea dredging in geographically confined areas, and includes deep-sea material which has been known only from few specimens and inadequate descriptions. The type localities for a number of early descriptions of *Verruca* (*sensu lato*) and *Scalpellum* (*sensu lato*) result from collections from "Talisman" cruises in the Atlantic from the Bay of Biscay to the Cape Verde Islands, "Travailleur" cruises in Mediterranean and the Bay of Biscay, and cruises by the Prince of Monaco in the Azores area (AURIVILLIUS, 1898; GRUVEL, 1900a, 1900b, 1902). The BALGIM material enables a better appreciation of specific variation covered by a number of nominate species described from these early cruises.

This study deals solely with systematics and broad biogeography, leaving bathymetry, hydrology and ecology for later consideration.

The paper is derived from a manuscript submitted to the *Bulletin du Muséum national d'Histoire naturelle*, Paris, prior to Brian FOSTER's untimely death. As the original manuscript incorporated a study of both Indian and Atlantic faunas, it was recommended that it be split, with each geographic area considered separately. The results for the Indian Ocean cruises has now been published (FOSTER & BUCKERIDGE, 1994). This manuscript incorporates any changes in cirripede phylogeny that have occurred since the preparation of FOSTER's manuscript, and further drawings have been added where necessary, ensuring that all described taxa are illustrated.

MATERIALS AND METHODS

The cruise and station data relevant to the various samples are given in Appendix A. In the following systematic treatment, the stations are referred to by the nomenclature on the labels included in the bottles, namely collecting gear and station number. The gear used was as follows: CP, beam trawl; DC, Charcot-Picard dredge; DR, rock dredge; DS, Sanders dredge; DW, Waren dredge; FA, Faubert bottom net trawl; PI, submersible dive or SCUBA diver.

Specimens were sorted at CENTOB and preserved in alcohol. They were examined with the aid of microscopy and dissection. Species regarded as new to science are given a full description. Others are illustrated from specimens, and their anatomy commented on where existing descriptions need amplification or to note points useful in identification. Illustrations of whole animals and shells were drawn with the aid of a drawing tube. Appendages were mounted in polyvinyl lactophenol and drawn with a camera lucida. Segments of cirri and caudal appendages were counted per rami, and where a single average figure is given it has been rounded up to an integer value for the complete rami.

All material is lodged in the Muséum national d'Histoire naturelle (MNHN), Paris.

SYSTEMATIC PART

LIST OF SPECIES

Family Poecilasmatidae Annandale, 1910

Octolasmis nierstraszi (Hoek, 1907)

Poecilasma kaempferi Darwin, 1851

Family Scalpellidae Pilsbry, 1907
Smilium acutum (Hoek, 1883)
Trianguloscalpellum regium (W. Thomson, 1873)
Trianguloscalpellum gigas (Hoek, 1883)
Arcoscalpellum michelottianum (Seguenza, 1876)
Arcoscalpellum crenulatum sp. nov.
Amigdoscalpellum praeceps (Hoek, 1907)
Verum ?minutum (Hoek, 1883)
Meroscalpellum bifurcatum (Zevina, 1973)
Verum novaezelandiae (Hoek, 1883)
Verum frillosum sp. nov.
Ornatoscalpellum stroemii (Sars, 1859)
Scalpellum scalpellum (Linnaeus, 1767)

Family Verrucidae Darwin, 1854
Verruca trisulcata Gruvel, 1900
Altiverruca gibbosa Hoek, 1883
Altiverruca vertica sp. nov.
Metaverruca recta (Aurivillius, 1898)

Family Pachylasmatidae Buckeridge, 1983
Pachylasma giganteum (Philippi, 1836)

Family Bathylasmatidae Newman & Ross, 1971
Bathylasma hirsutum (Hoek, 1883)

Family Balanidae Leach, 1817
Megabalanus tulipiformes (Ellis, 1758).

Family POECILASMATIDAE Annandale, 1910

Octolasmis nierstraszi (Hoek, 1907)
(Fig. 1A)

MATERIAL. — CORINDON II: station 263, Strait of Makassar, 80 m (1 specimen).

RECORDS. — HOEK, 1907a: 21, 19 stations East Indies, 16-120 m; NILSSON-CANTELL, 1921: 268, Japan, 135 m; NILSSON-CANTELL, 1927: 762, Persian Gulf; NILSSON-CANTELL, 1934a: 60, Malaysia, 73 m; BROCH, 1931: 40, Kei Is, 38-50 m; HIRO, 1937a: 414, Japan, 24 m (*i.e.*, Persian Gulf, Malaysia to Japan, 16-135 m). FOSTER & BUCKERIDGE, 1994: 348, La Réunion, 75-92 m. On hydroids, etc.

REMARKS

The bilobed tergum and narrowly split scutum clearly distinguish this species, but it is apparent that there is variation in the shape of the basal arm of the scutum, in some cases making the scutum tri-lobed.

Poecilasma kaempferi Darwin, 1851
(Fig. 1B)

MATERIAL. — BALGIM: CP156, 1135 m (1 specimen); DW157, 1108 m (1).

REMARKS

This is a frequently reported species (see ZEVINA, 1982: 98-100 for full records and synonymies; also ROSELL, 1989: 22 for a new Philippines record), as an epizooite on benthic invertebrates, particularly decapod crustaceans, circumglobal, 126-1885 m. The subspecies *aurantia* Darwin, *dubium* Hoek, *litum* Pilsbry and *novaeangliae* Pilsbry are probably ecotype variants. In specimens collected from the same lobster or crab in New Zealand waters, there is a wide range of shell variations, seemingly associated with position on, or proximity to mechanical disturbances from the various appendages of the host.

Family SCALPELLIDAE Pilsbry, 1907

Subfamily CALANTICINAE Zevina, 1978

Smilium acutum (Hoek, 1883)
(Fig. 1C)

MATERIAL. — BALGIM: CP65, 1805 m (1 specimen); CP68, 2035 m (3); CP69, 2028 m (23); DR82, 355 m (4). BIOGAS V: CP07 (off Cape Finisterre), 2170 m (5). EPI I: CP38 (Gulf of Gascogne), 2100 m (1); CP39, 2175 m (1). BIOCYAN II (Bay of Biscay): PL18, 2000 m (3).

RECORDED DISTRIBUTION. — Circum-global, 61-2480 m. See ZEVINA, 1981: 82 and NEWMAN & ROSS, 1971: 38 for synonymies and references; also ROSELL, 1989: 19, Philippines, 882-770 m.

REMARKS

This widely distributed, frequently encountered and distinctive barnacle was first described by HOEK (1883) from material from both the North Atlantic and the South-West Pacific Oceans. It occurs on a wide variety of substrata, including hydroids, crustaceans, spicules. It nicely

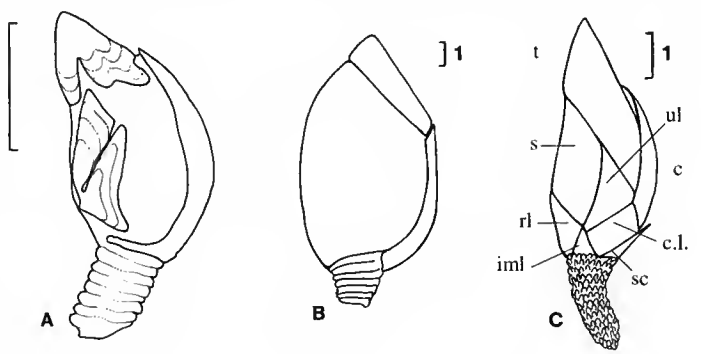

FIG. 1. — Poecilasmatidae and Scalpellidae: A, *Octolasmis nierstraszi* CORINDON II Stn 263. B, *Poecilasma kaempferi* BALGIM, CP156. C, *Smilium acutum* BALGIM, CP69. Scales in mm. Capitular plates: c, carina; s, scutum, t, tergum, ul, upper latus, c.l., carinolatus, rl, rostrolatus, iml, inframedian latus, sc, subcarina. *Poecilasmatidae et Scalpellidae: A,* Octolasmis nierstraszi *CORINDON II Stn 263. B,* Poecilasma kaempferi *BALGIM, CP156. C,* Smilium acutum, *BALGIM, CP69. Échelles en mm. Plaques capitulaires : c, carina ; s, scutum, t, tergum, ul, latus supérieur, c.l., carinolatus, rl, rostrolatus, iml, latus inframédian, sc, subcarina.*

demonstrates the degree of variation in shell morphology (mostly ontogenetic change in capitulum dimensions — the capitulum becoming more elongate and the tergum reflexed, the peduncle with more numerous closely compact scales), and a circum-global distribution in moderately deep water.

The collection of 41 specimens from 8 stations (355-2175 m) in the North Atlantic Ocean of this report is comparable to the 199 specimens from 23 stations (391-1220 m) resulting from New Zealand Oceanographic Institute sampling in New Zealand waters (FOSTER, 1978).

Subfamily SCALPELLINAE Pilsbry, 1907

Trianguloscalpellum regium (W. Thomson, 1873)
(Figs 2A-D, 3)

MATERIAL. — BIOGAS VII (Bay of Biscay): CP28, 3380 m (2 specimens). BIOGAS VIII (Bay of Biscay): CP30, 3100 m (21).

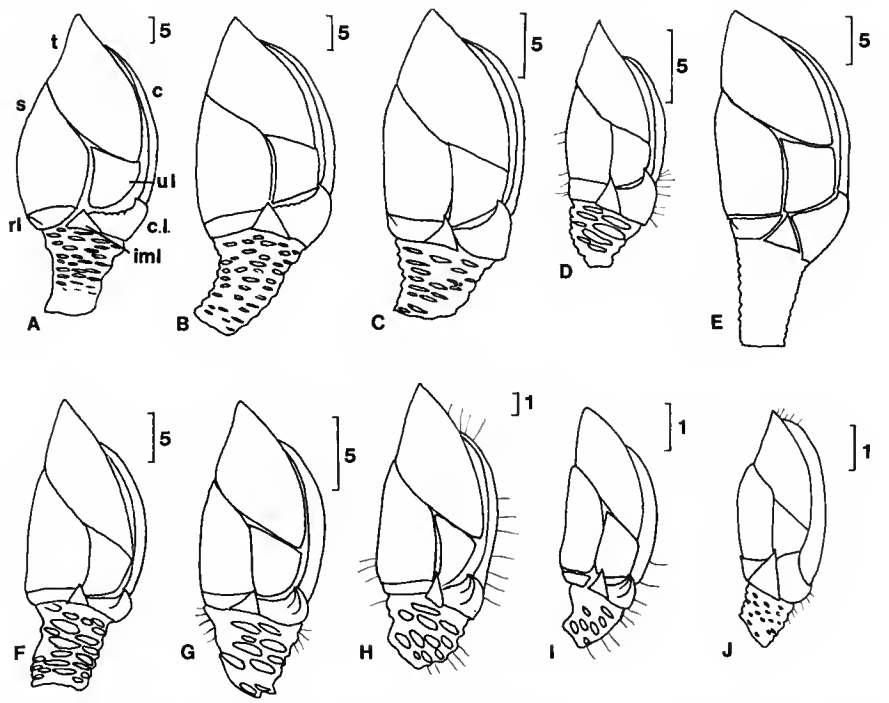

FIG. 2. — Scalpellidae: A-D: *Trianguloscalpellum regium*. A, BIOGAS VII CP30 (47.0 mm c.l.). B, BIOGAS VII CP28, (36.0 mm c.l.). C, BIOGAS VII CP30 (19.0 mm c.l.). D, BIOGAS VII CP30 (11.0 mm c.l.). E, *Trianguloscalpellum gigas* GASCOR, CP42 (22.0 mm c.l.). F-I, *Arcoscalpellum michelottianum* BAGIM, CP95, F, *ditto* (23.0 mm c.l.). G, *ditto*, (14.5 mm c.l.). H, *ditto*, (10.2 mm c.l.). I, *ditto* (3.6 mm c.l.). Scales in mm.

Scalpellidae: A-D: Trianguloscalpellum regium. *A, BIOGAS VII CP30 (l.c. = 47,0 mm). B, BIOGAS VII CP28, (l.c. = 36,0 mm). C, BIOGAS VII CP30 (l.c. = 19,0 mm). D, BIOGAS VII CP30 (l.c. = 11,0 mm). E,* Trianguloscalpellum gigas *GASCOR, CP42 (l.c. = 22,0 mm). F-I,* Arcoscalpellum michelottianum *BAGIM, CP95, F,* dito *(l.c. = 23,0 mm). G,* dito, *(l.c. = 14,5 mm). H,* dito, *(l.c. = 10,2 mm). I,* dito *(l.c. = 3,6 mm). Échelles en mm.*

RECORDS. — THOMSON, 1873: 347, and HOEK, 1883: 106, North Atlantic, 5029-5212 m; GRUVEL, 1920: 30, off Cape Finisterre, 2779 m. Not PILSBRY, 1907a: 28, off Chesapeake Bay, 3740 m, = *T. gigas*, see below. As *molle* Aurivillius, 1898: 191, Azores 845-1023 m; and GRUVEL, 1920: 29, Azores, 4020 m. As var. *ovale* Hoek, 1883: 109, North Atlantic, 5212 m. As var. *latidorsum* Pilsbry, 1907a: 29, off New York, 1812-2940 m. (*i.e.*, North Atlantic, 845-5212 m). FOSTER & BUCKERIDGE, 1994: 355, La Réunion, 4030 m.

REMARKS

The illustrations of 4 specimens from CP30 show the change in capitulum form with growth. The plates maintain close approximation, except for the carinolatera which become more widely displaced from each other below the carina. There is a widening of the lateral aspect of the capitulum to an oval form in larger specimens. The species can reach a large size (47 mm capitulum length and 33 mm peduncle length in the present material). The plates are robust, brownish, with relatively smooth surfaces and faint growth ridges. The carina has obvious lateral sides. The integument between the plates is variously hirsute. The lower latera possess a low profile, with the apex of the carinolatus characteristically curled across the base of the carina to slightly overlap the upper latus at this position in smaller specimens.

The mandible is tridentoid. The segmentation of the posterior cirri increases with size of the animal (Fig. 3); that of cirrus I and the caudal appendages, with lower numbers of segments,

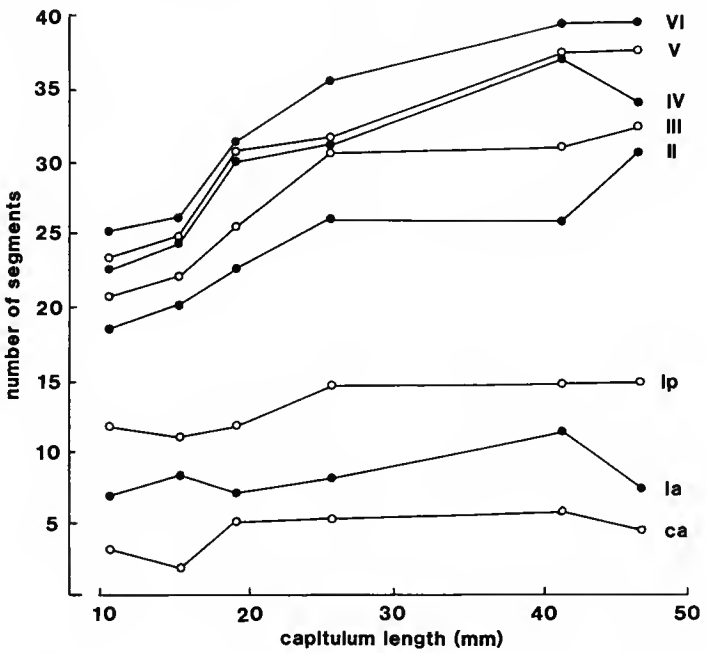

FIG. 3. — Scalpellidae: *Trianguloscalpellum regium* BIOGAS VII CP30. Mean numbers of segments of rami as a function of size of specimen. For anterior (a) and posterior (p) rami of cirrus I (average of 2); all rami of cirus II-VI (average of 4); both caudal appendages (ca), average of 2.

Scalpellidae: Trianguloscalpellum regium *BIOGAS VII CP30. Nombres moyens de segments des rames en fonction de la taille des spécimens. Rames antérieure (a) et postérieure (p) du cirrhe I (moyenne de 2 relevés) ; ensemble des rames des cirrhes II-VI (moyenne de 4 relevés) ; ensemble des appendices caudaux (ca), moyenne de 2 relevés.*

much more constant. The caudal appendage reaches about 0.5 times the length of the pedicle of cirrus VI. Penis absent. Complemental males carried in interscutal pouches.

Trianguloscalpellum gigas (Hoek, 1883)
(Fig. 2E)

MATERIAL. — GASCOR (Bay of Biscay): CP42, 3815 m (3 specimens).

RECORD. — HOEK, 1883: 102, mid North Pacific, 3749 m.

REMARKS

This species is similar to *T. regium*, but is distinguished by the less rounded profile of the capitulum, with a proportionally longer upper latus and scutum. The plates are less glossy, and the carina is rounded, without lateral sides. Most significantly, this species is a hermaphrodite; it has a penis. The type specimen in the British Museum of Natural History conforms to this.

HOEK (1883) thought that there was a close relationship between *T. gigas* and *T. darwini* (Hoek). This latter species was described on the basis of a single large specimen (48 mm capitulum length, 31 mm peduncle length) from off Chile in the South-East Pacific. Examination of this specimen in the British Museum shows it lacks a penis, and it is more likely that HOEK's *Scalpellum darwini* is *T. regium*, and that PILSBRY's (1907) and ZEVINA's (1981: 309) specimens are *T. gigas*. Both species would thus occur in deep seas around the world.

Arcoscalpellum michelottianum (Seguenza, 1876)
(Figs 2F-H, 4)

MATERIAL. — BALGIM: CP10, 1592 m (14 specimens); CP17, 1470 m (3); CP63,1510 m (27); CP65, 1805 m (5); CP68, 2035 m (10); CP69, 2028 m (2); CP92, 1182 m (15); CP95, 1378 m (25); CP97, 1515 m (9); CP99, 1870 m (10). EPI VI: KG229 (off Brest), 2160 m (1).

RECORDS. — NEWMAN & ROSS, 1971: 71, off Greenland, 3404-3422 m and off South Carolina, 3010 m; RAO & NEWMAN, 1972, Jonston Atoll, Mid-Pacific Ocean; ROSELL, 1989: 17, Philippines, 682-770 m. As *velutinum* Hoek, 1883: 96, off Cape St Vincent, 1656 m and off Tristan da Cunha, 2606 m; GRUVEL, 1902: 56, off Canary Is, 882-2000 m; PILSBRY, 1907a: 26, western North Atlantic, 64-1962 m; not ANNANDALE, 1913: 229, India, 786 m, = *annandale* Calman, 1918: 109; CALMAN, 1918: 109, Java-Australia, 732-1280 m, and Aden-Zanzibar, 1097 m; GRUVEL, 1920: 27, Azores, 1331 m, off Nova Scotia, 1458 m; BARNARD, 1925: 1, South Africa; NILSSON-CANTELL, 1927: 743, Singapore; BROCH, 1931: 18, off Hong Kong, 760 m; STUBBINGS, 1936: 28, Zanzibar, 690-762 m; ZEVINA, 1972: 43, South-East Pacific, 660-700 m. As *eximium* Hoek, 1883: 100, off Tristan da Cunha, 1828 m. As *sordidum* Aurivillius, 1898: 190, off New Foundland, 1267 m and off Portugal, 2028 m; GRUVEL, 1920: 27, Canary Is, 1098 m. As *erectum* Aurivillius, 1898: 192, Azores 1135-1165 m. As *alatum* Gruvel, 1900a: 192, 1902: 57. Distribution is, therefore, circumglobal, 64-3422 m. Long known as *Arcocalpellum velutinum* Hoek, 1883 but synonymised with fossils by WITHERS (1953).

REMARKS

This species is commonly encountered in the Atlantic Ocean (for full synonymy see ZEVINA, 1981: 343 and NEWMAN & ROSS, 1971: 71). NEWMAN & ROSS (1971) gave much needed description of young stages. To further augment the description, particularly with regard to changes that occur during growth, 15 of the specimens from CP95 were dissected, and 4 are illustrated in Figure 2.

This barnacle is hirsute, particularly in young stages, finely so in the larger specimens. The plates are approximate, the capitulum elongate because of an elongate scutum and upper latus (compared with *T. gigas* and *T. regium*). The lower latera are proportionately low, and the apeces of the inframedian latus projects above the upper line of the rostro- and carinolatera. The apeces of the carinolatera curve towards but do not overlap with the lower carinal border of the upper latus.

Mandibles tridentoid except in one large specimen (21 mm capitulum length) in which a small extra tooth occurs below the upper tooth. Penis absent. The numbers of segments in the rami of the cirri and caudal appendage increase with size of the individuals (Fig. 4). It is interesting to compare the numbers and trends with those of *T. regium* (Fig. 3). Size for size it is not possible to distinguish the two species on this sort of numerical data.

The material includes a solitary juvenile from CORINDON II Stn 248 at 170 m; it is clearly scalpelline, and might be *A. michelottianum*, but without co-occurring adults, identification is uncertain. Isolated juvenile stages of any scalpelline are difficult to identify, because of the similar arrangement of plates in juveniles.

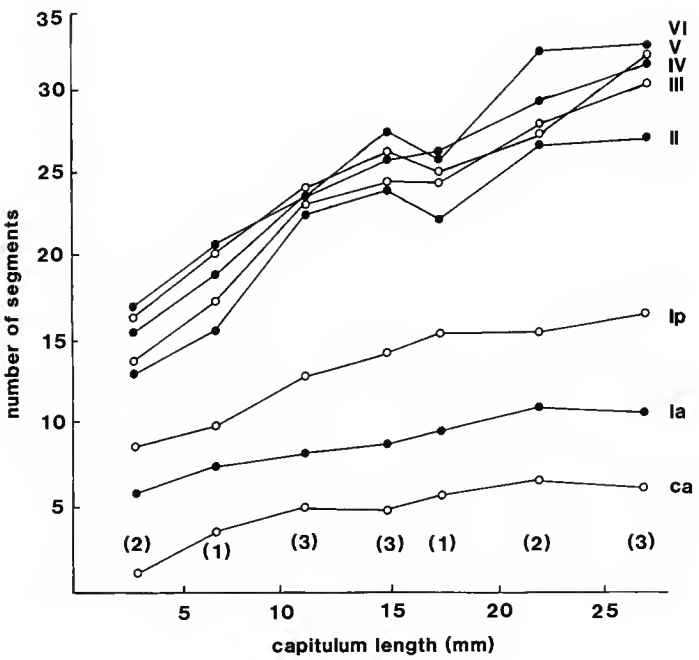

FIG. 4. — Scalpellidae: *Arcoscalpellum michelottianum* BALGIM, CP95. Mean numbers of segments of rami as a function of size of specimen. Average of rami for the numbers of specimens shown above the abscissa.

Scalpellidae : Arcoscalpellum michelottianum *BALGIM, CP95. Nombres moyens de segments des rames en fonction de la taille des spécimens. Nombre moyen de rames en fonction du nombre de spécimens examinés indiqué au dessus de l'abscisse.*

Arcoscalpellum crenulatum n. sp.
(Fig. 5A-F)

MATERIAL. — BIOGAS VIII (Bay of Biscay): CP30, 3100 m (2 specimens: holotype MNHN Ci 2132; paratype MHNH Ci 2133).

DESCRIPTION OF HOLOTYPE

15.2 mm capitulum length. Capitulum higher than wide. Tergum triangular, apex erect. Carina simply bowed, flat roofed, with strong longitudinal ridges on each side. Scutum quadrangular, apex acute and curved over the tergum, upper margin concave and with secondary growth flange towards the tergum, upper latus margin hollowed out below the upper angle for reception of apex of upper latus. Upper latus pentagonal, with concave margin towards scutum, bearing a narrow rib along this margin, and lower margin mostly abutting the rostrolatus but also touching the inframedian latus. Carinolatus pentagonal, carinal margin concave, and occludent margin projecting slightly beyond the carina below the carina. Inframedian latus triangular, penetrating in these specimens, to the lowest corner of the upper latus. Rostrolatus rectangular, with the lateral margin abutting both the inframedian latus and the upper latus, the margin against the scutum crenulate to the extent of the abutment with the ridge of the upper latus.

Cirri I and II with anterior rami slightly shorter than posterior rami; segments of Ia 1.5 times as wide as those of posterior ramus. Caudal appendages as long as pedicle of cirrus VI. Intermediate segments of posterior cirri with 3 pairs of setae on anterior edge; a single spine on the posterior edge of posterior ramus only.

Segment counts, anterior ramus first:

I	II	III	IV	V	VI	ca
8,9	12,17	17,19	21,17+	23,22	22,26	5
7,11	14,16	18,19	16+,16+	21,21	22,25	5

REMARKS

This species closely resembles *Amigdoscalpellum aurivilli* (Pilsbry) from off Cape Hatteras, and also *Arcoscalpellum pertosum* Foster from New Zealand in the way the plates are apposed.

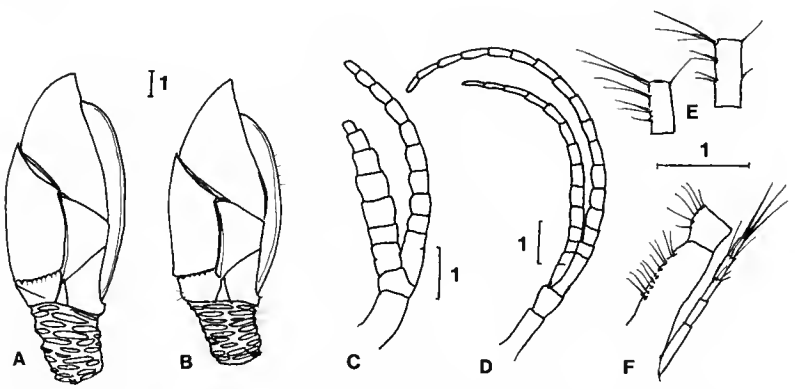

FIG. 5. — Scalpellidae: A-F, *Arcoscalpellum crenulatum* sp. nov. A, BIOGAS VIII, CP30 holotype (15.2 mm c.l.); B, *ditto*, paratype, (13.0 mm c.l.); C, cirrus I; D, cirrus II; E, intermediate segments cirrus VI; F, pedicle cirrus VI and caudal appendage.

Scalpellidae : Arcoscalpellum crenulatum *sp. nov. : A, BIOGAS VIII, CP30 holotype (15,2 mm l.c.); B,* dito, *paratype, (13,0 mm l.c.) ; C, cirrhe I ; D, cirrhe II ; E, segments intermédiaires du cirrhe VI ; F, partie basale du cirrhe VI et appendice caudal.*

However, the crenulate upper margin of the rostrolatus, the penetration of the inframedian latus all the way to the upper latus, and the relatively short occludent margins of the carinolatera below the carina, set the CP30 specimens apart. They are also from deeper water than the above named species.

Amigdoscalpellum praeceps (Hoek, 1907)
(Fig. 6A)

MATERIAL. — BIOGAS VIII (Bay of Biscay): CP30, 3100 m (1 specimen). BIOGAS XI (Bay of Biscay): CP35, 4720 m (I).

RECORD. — HOEK, 1907a: 114, East Indies, 411 m. FOSTER & BUCKERIDGE, 1994: 356, La Réunion, 1660-2970 m.

REMARKS

This slender barnacle possesses lightly sculptured plates which show, through ontogeny, a widening of the carinal tergal interspace and a reduction of the inframedian latus from full occupation of the space between the rostro- and carinolatera to about 0.2 times of it and displaced outwards in large specimens (FOSTER & BUCKERIDGE, 1994).

Verum? minutum (Hoek, 1883)
(Fig. 6B-F)

MATERIAL. — BALGIM: CP68, 2077 m (13 specimens); CP69, 2028 m (3); CP99, 1870 m (3).

RECORD. — HOEK, 1883: 113, South-East Pacific, 2652 mm; STUBBINGS, 1936: 28, off Zanzibar, 802 m. FOSTER & BUCKERIDGE, 1994: 358, La Réunion, 1850-3520 m.

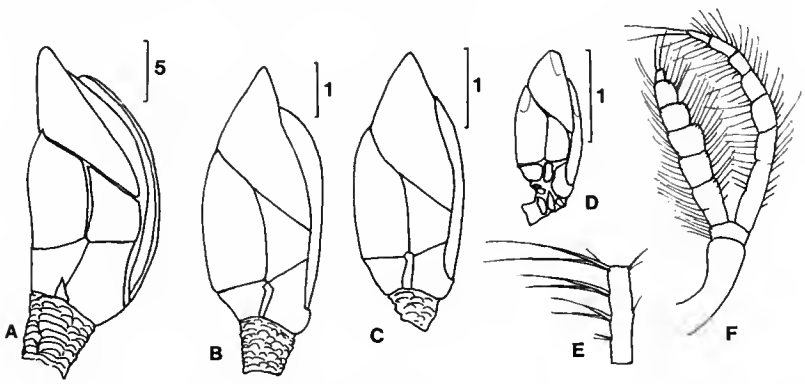

FIG. 6. — Scalpellidae: A, *Amigdoscalpellum praeceps* BIOGAS XI, CP35 (27.8 mm c.l.). B-F, *Verum minutum*: B, BALGIM, CP68 (5.8 mm c.l.). C, BALGIM CP69, (3.8 mm c.l.). D, BALGIM, CP99 (2.2 mm c.l.). E, BALGIM, CP68 (4.8 mm c.l.) cirrus I. F, *ditto*, intermediate segment posterior ramus cirrus VI. Scales in mm.

Scalpellidae: A, Amigdoscalpellum praeceps *BIOGAS XI, CP35 (l.c. = 27,8 mm). B-F,* Verum minutum*: B, BALGIM, CP68 (l.c. = 5,8 mm). C, BALGIM CP69, (l.c. = 3,8 mm). D, BALGIM, CP99 (l.c. = 2,2 mm). E, BALGIM, CP68 (l.c. = 4,8 mm) cirrhe I. F,* dito, *segments intermédiaires de la rame postérieure du cirrhe VI. Échelles en mm.*

REMARKS

Barnacle small, slender, non-hirsute, with smooth, non-striated plates, and faint growth ridges. Scutum and upper latus elongate, without secondary growth flanges. Carina slightly bowed in upper part. Tergum elongate, apex not curved. Carinolatus slightly higher than wide. Rostrolatus quadrangular, with slight convexity on occludent margin. Inframedian latus very narrow, slightly wider near the upper extremity, umbo apical, and with very short scutal and upper latus margins. The apex of the inframedian latus is club-shaped, tipped towards the rostral margin, and displaced slightly from it in larger specimens (FOSTER & BUCKERIDGE, 1994).

Meroscalpellum bifurcatum (Zevina, 1973)
(Fig. 7A, B)

MATERIAL. — BIOGAS XI: CP35 (off Tristan da Cunha), 4720 m (1 specimen). WALDA: CY09 (off Angola), 4613 m (1).

RECORD. — ZEVINA, 1973: 1003, Indian Ocean, 4151 m (in ZEVINA, 1981: 175).

REMARKS

This is one of the scalpellines which show in the adult form variously reduced plates and marked cuticular spaces between these plates. ZEVINA (1981) gives illustrations of 11 mm and 20 mm capitulum length specimens. Not only does the degree of capitular plate coverage decrease in larger specimens, but the shapes of the plates themselves (except the carina) are increasingly irregular.

Similar sequences of capitulum variations and changes have been documented for *Neoscalpellum debile* (Aurivillius) by ZEVINA (1981) and for *Litoscalpellum intermedium* (Hoek) by FOSTER (1980). These instances serve as examples of the problems associated with a taxonomy based on isolated specimens, and possible confusions among generic assignments.

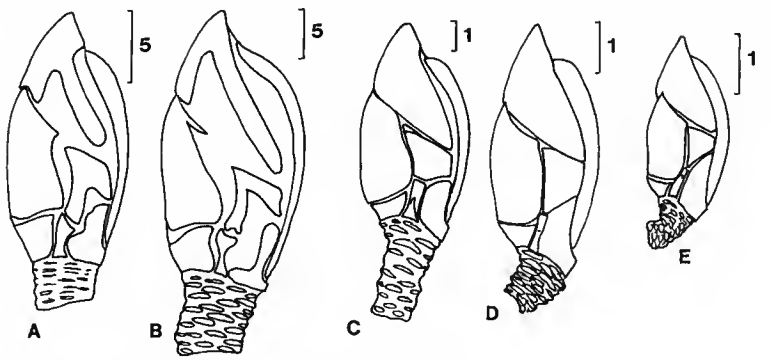

FIG. 7. — Scalpellidae: A, *Meroscalpellum bifurcatum* WALDA, CY09 (16.2 mm c.l.). B, *ditto*, BIOGAS XI, CP35 (29.6 mm c.l.). C-E, *Verum novaezelandiae*: C, EPI 1, CP39 (7.6 mm c.l.). D, *ditto* (6.0 mm c.l.). E, *ditto* (4.0 mm c.l.). Scales in mm. *Scalpellidae: A,* Meroscalpellum bifurcatum *WALDA, CY09 (l.c. = 16,2 mm). B,* dito, *BIOGAS XI, CP35 (l.c. = 29,6 mm). C-E,* Verum novaezelandiae*: C, EPI 1, CP39 (l.c. = 7,6 mm). D,* dito *(l.c. = 6,0 mm). E,* dito *(l.c. = 4,0 mm). Échelles en mm.*

Verum novaezelandiae (Hoek, 1883)
(Fig. 7C-E)

MATERIAL. — BALGIM: CP10, 1592 m (1 specimen). EPI I: CP38 (Bay of Biscay), 2100 m (14); CP39, 2100 m (7). CORINDON II (Makassar Strait): Stn 236, 1730 m (1).

RECORDS. — HOEK, 1883: 124, New Zealand, 1280 m; GRUVEL, 1902: 54, off Portugal, 2400-2500 m; ANNANDALE, 1908 &1913: 231, off Andaman Is, 896-2800 m; CALMAN, 1918: 123, Gulf of Aden, 2195 m; WELTNER, 1922: 71 East-African coast, 1289-1644 m; FOSTER, 1978: 65 & 1980: 530, New Zealand, 455-2431 m.

REMARKS

This species was well represented in collections from New Zealand (FOSTER, 1978, 1980). It is clear that this deep water species is widespread. The present records confirm the Atlantic Ocean records of GRUVEL (1902).

V. novaezelandiae is recognised by the very slender capitulum in which the carinolatus is markedly elongated to match a pronounced apical growth of the inframedian latus. This latter plate remains narrow, with clear edges to the upper latus and scutum. With growth, the umbo of the inframedian latus is placed closer to the basal margin. In some specimens the rostrolatus is very narrow, particularly if growth of the peduncle has been bent to the rostral side.

Appendage counts for CP39 specimens are as follows:

cl(mm)	Ia	Ib	II	III	IV	V	VI	ca
4.8	6	8	14	14	15	17	17	4
6.0	7	9	14	17	16	18	20	5
7.6	8	11	15	19	–	24	–	6

The appendage details conform to New Zealand specimens (FOSTER, 1978).

Verum frillosum nov. sp.
(Fig. 8)

MATERIAL. — BIOGAS VII: CP28 (Bay of Biscay), 3380 m (1 specimen, holotype MNHN Ci 2135).

DESCRIPTION OF HOLOTYPE

18.0 mm capitulum length. Peduncle only partially intact, scales wide. Tergum triangular, apex recurved, dorsal margin notched for reception of carina. Carina simply bowed. Scutum pentagonal, upper margin with secondary growth flange against tergum, lateral margin slightly concave, lower margin sinuous in conjunction with rostro- and inframedian latus. Inframedian latus hourglass-shaped, upper part wider than lower part, with sinuous margins to scutum and upper latus. Upper latus pentagonal, upper margin with secondary growth flange towards apex, margins to inframedian- and carinolatus sinuous. Carinolatus higher than wide, upper margin sinuous, occludent margin beneath carina short. Rostrolatus broadly quadrangular.

Mandible tridentoid, lower angle acuminate. Maxillule with 2 stout spines at upper angle, bunch of shorter spines at lower angle. Cirrus I with anterior ramus intermediate segments 2 times

width of those of posterior ramus. Mean numbers of segments in cirri as follows, anterior ramus first:

I	II	III	IV	V	VI	ca
8,12	16,19	20,20	24,24	24,24	25,25	3

Intermediate segments cirrus VI with 5 pairs of setae on anterior edge, no setae midway on posterior edge. Caudal appendages 2-3 segments, just longer than pedicle of cirrus VI.

REMARKS

This barnacle is similar to *Verum constrictum* but lacks constricted rostrolatera, and the growing edges of the upper latus, rostrolatus, carinolatus and inframedian latus are sinuous in accord with the alternating and interlocking growth ridges of these plates.

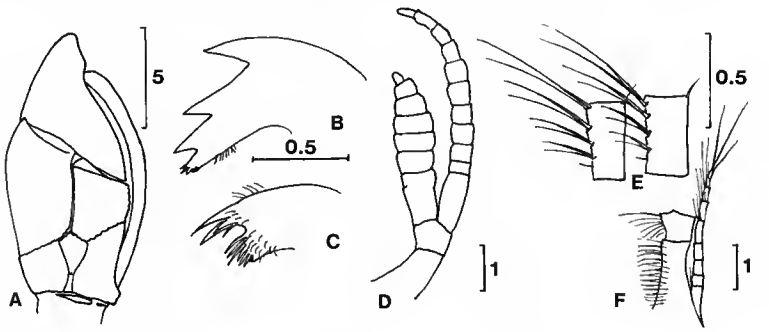

FIG. 8. — Scalpellidae: *Verum frillosum* sp. nov. BIOGAS VII, CP28: A, capitulum holotype (18.0 mm cl). B, mandible. C, maxillule. D, cirrus I. E, intermediate segments anterior and posterior rami cirrus VI. F, pedicle cirrus VI and caudal appendage. Scales in mm.

Scalpellidae: Verum frillosum *sp. nov. BIOGAS VII, CP28: A, capitulum holotype (Cl = 18.0 mm). B, mandible. C, maxillule. D, cirrhe I. E, segments intermédiaires des rames antérieure et postérieure du cirrhe VI. F, partie basale du cirrhe VI et appendice caudal. Échelles en mm.*

Ornatoscalpellum stroemii (M. Sars, 1859)
(Fig. 9A)

MATERIAL. — BALGIM: DR82, 355 m (3 specimens).

RECORDS. — HOEK, 1883: 73, northern Atlantic Ocean, 152-944 m; PILSBRY, 1907a: 21, North American fishing banks, 143-214 m; and other references in ZEVINA, 1981: 111. As *pressum* Pilsbry, 1907a: 23, Le Havre Bank, 549 m. As *septentrionale* Aurivillius, 1892: 128 and 1894: 51, North Sea, 590-890 m. As *erosum* Aurivillius, 1892: 119 and 1894: 52, North Atlantic, 1744 m. As *obesum* Aurivillius, 1892: 119 and 1894: 56, North Sea, 110 m. As *luridum* Aurivillius, 1892: 120 and 1894: 59, Baffin Bay, 309 m.

REMARKS

The synonymy of 4 of AURIVILLIUS' (1892, 1894) and 3 of PILSBRY's (1907a) names within *O. stroemii* (see ZEVINA, 1981: 111) illustrates the variation within at least some of the scalpelline

species, and the tendency to name this variation by early taxonomists. PILSBRY (1907a: 21) was troubled about HOEK's (1883) illustration of the species, particularly the latter giving the impression that the scutum, inframedian latus and upper latus have subcentral umbos, and also with the proportions of the upper latus. There may have been some over-artistry in HOEK's plates (not confined to this species), but the fact is that during ontogeny the position of the umbo of the inframedian latus becomes progressively displaced from the apex, and both the upper latus and carina also develop apical growth zones. The rectangularly bent carina, in its upper part, results from displacement of the umbo, as it is in *Scalpellum scalpellum*.

This is a relatively shallow water scalpelline, often collected in fishing trawls. Stn DR82 is off the Morocco coast, and is a southernmost record of the species.

Scalpellum scalpellum (Linnaeus, 1767)
(Fig. 9B-D)

MATERIAL. — BALGIM: CP103, 347 m (21 specimens).

RECORDS. — North-East Atlantic, Norway (68°N) to Congo (6°S), 50-366 m; Mediterranean (RELINI, 1980: 93, Italian seas, to 400 m). See ZEVINA, 1981: 95 for synonymies and references.

REMARKS

Of all the 18 species considered in this collection, this is the only one in which the umbo of the scutum is displaced from the apical position. The relatively square lateral shape of the capitulum is produced by considerable subapical displacement of the umbos of the carina and upper latus.

This is a relatively shallow occurring barnacle. It is frequently encountered on hydroids and hydroid-like growths on trawling grounds, and is a well-known barnacle to European marine naturalists. This is the only known species of the Scalpellinae from the Mediterranean Sea (RELINI, 1980).

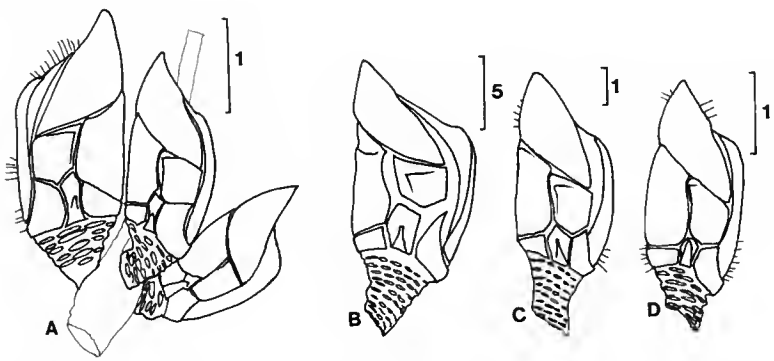

FIG. 9. — Scalpellinae: A, *Ornatoscalpellum stroemii* BALGIM, DR82, group, largest 5.5 mm c.l. B, *Scalpellum scalpellum* BALGIM, CP103 (13.5 mm c.l.). C, *ditto* (6.2 mm c.l.). D, *ditto* (3.0 mm c.l.). Scales in mm.

Scalpellinae : A, Ornatoscalpellum stroemii *BALGIM, DR82, plus grand individu du groupe l.c. = 5,5 mm. B,* Scalpellum scalpellum *BALGIM, CP103 (l.c. = 13,5 mm). C,* dito *(l.c. = 6,2 mm). D,* dito *(l.c. = 3,0 mm). Échelles en mm.*

Family VERRUCIDAE Darwin, 1854

Discussion

There are 83 named species of verrucid (Buckeridge, 1994, Foster & Buckeridge, 1994). They are asymmetrical sessile barnacles having a shell wall composed of carina, rostrum, fixed scutum and fixed tergum, and an operculum of movable tergum and movable scutum. Nomenclature of these plates is shown in Fig. 10A. A fuller discussion of the morphology and genera is available in Buckeridge (1994).

The present material is particularly rich in verrucids, both in the number of determined species (4) and individuals (420). Furthermore, the BALGIM collections are in the locality from which Aurivillius (1898) and Gruvel (1900b, 1902, 1905, 1912) named and/or described many species.

Verruca trisulcata Gruvel, 1900
(Figs 10, 11, 12)

Material. — BALGIM: CP90, 890 m (9 specimens); CP91, 948 m (4); CP92, 1182 m (70); CP95, 1378 m (22); CP156, 1135 m (252); DW157, 1108 m (28); CP160, 1350 m (9).

Records. — Gruvel, 1900b: 243; 1902: 96; 1920: 44, Azores, 998 m. Gruvel, 1912: 348, Cape Spartel (Straits of Gibraltar), 622 m. As *imbricata* Gruvel, 1900b: 244, 1902: 105, Azores, 441 m. As *striata* Gruvel, 1900b: 244; 1902: 98, Cape Verde I, 633 m. As *radiata* Gruvel, 1900b: 262, 1902: 94, Canaries, 912 m; Foster & Buckeridge, 1994: 363, La Réunion, 980-1690 m.

Remarks

A range of shell forms is illustrated to show the range from low splayed (half as high as wide) to quite upstanding (higher than wide) posture. Of 26 shells from CP92 (Fig. 11) the height: width ratio ranges from 0.5 to 1.0, with no significant trend with size of specimen. Also, with growth, the number of interlocking ribs between the movable tergum and scutum, and between the carina and rostrum, increases from 1 in juveniles to 4 in specimens of about 6 mm rostrocarinal length. A characteristic feature of the shell is the particularly wide superior rib on the rostrum. The apeces of the rostrum and carina are never turned inwards. The "back" view (*i.e.* of the fixed tergum and scutum) is highly variable; tall with easily discernable alae and radial growth areas, or squat and contorted depending on irregularities of substratum. Movable scutum apex curved over the superior articular groove, with a moderately deep apical pit internally. Movable tergum broadly quadrangular, 1.5 times width of scutum, lower angle protruding as apical ridge.

Mandible tridentoid, with a pectinate lower edge. Maxillule with an irregular cutting edge, the lower angle protuberant (a feature common in verrucids). Cirrus I anterior ramus just over 0.5 times length of posterior ramus. Cirrus II anterior ramus less than 0.5 times length of posterior ramus. Cirrus III-VI with subequal rami. Caudal appendage about 0.66 times length of cirrus VI. Plots of the numbers of segments per rami (Figure 12) show increasing numbers of segments in all rami with increasing size of the specimen. Caudal appendage 0.5 times length of cirrus VI.

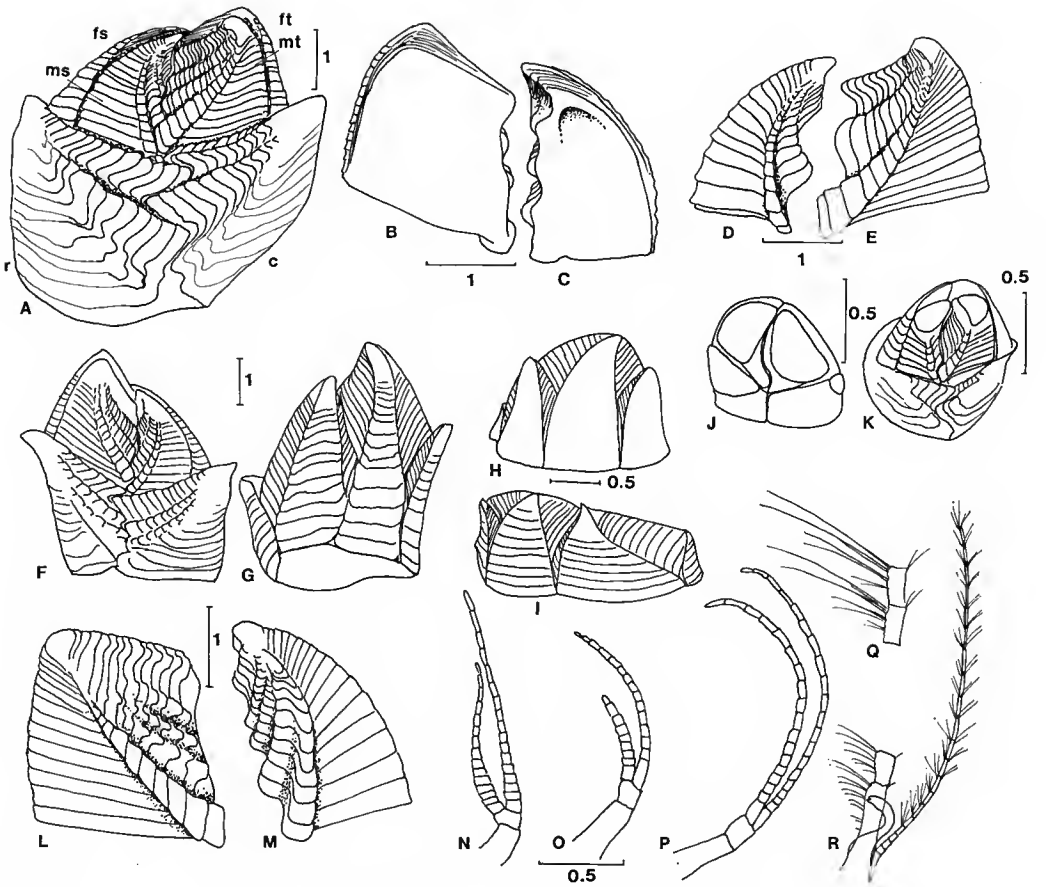

FIG. 10. — Verrucidae: *Verruca trisulcata*. A, BALGIM, CP160 (5.5 mm rcl). B, C, opercula, inner views, specimen A. D, E, opercula, outer views, BALGIM, CP160. F, G, "front" and "rear" views, BALGIM CP92 (5.0 mm rcl). H, I, "rear" views of others BALGIM CP92; same scale. J, juvenile, BALGIM, CP160 (0.8 mm rfcl). K, post-juvenile, BALGIM CP90 (1.8 mm rcl). L, M, operculA, outer views BALGIM, CP90. N, cirrus I, BALGIM, CP90 (from 5.9 mm c.l.). O, cirrus II, *ditto*. P, cirrus III, *ditto*. Q, intermediate segment cirrus VI, *ditto*. R, pedicle cirrus VI, penis and caudal appendage, *ditto*. N-R to same scale. Scales in mm. Shell plates: c, carina; fs, fixed scutum; ft, fixed tergum; ms, movable scutum; mt, movable tergum; r, rostrum. rcl = umbos of rostrum to carina length.

Verrucidae : Verruca trisulcata. *A, BALGIM, CP160 (lrc = 5,5 mm). B, C, opercule, vues internes, spécimen A. D, E, opercules, vues externes, BALGIM, CP160. F, G, vues antérieure et postérieure, BALGIM CP92 (lrc = 5,0 mm). H, I, vues postérieures des autres spécimens BALGIM CP92 ; même échelle. J, juvénile, BALGIM, CP160 (lrc = 0,8 mm). K, post-juvénile, BALGIM CP90 (lrc = 1,8 mm). L, M, opercule, vues externes BALGIM, CP90. N, cirrhe I, BALGIM, CP90 (lrc = 5,9 mm). O, cirrhe II,* dito. *P, cirrhe III,* dito. *Q, segment intermédiaire du cirrhe VI,* dito. *R, partie basale du cirrhe VI, pénis et appendice caudal,* dito. *N-R dessinés à la même échelle. Échelles en mm. Plaques de la coquille : c, carène ; fs, scutum fixe ; ft, tergum fixe ; ms, scutum mobile ; mt, tergum mobile ; r, rostre. lrc = distance séparant l'umbo du rostre de la carina.*

The type locality for *V. striata* is also in the Atlantic Ocean. It seems unavoidable that *trisulcata*, *imbricata*, *striata* and *radiata* are synonymous. Because the number of articular ribs on the movable tergum is not constant, nor is the overall shell shape, it may be that *V. grimaldi*

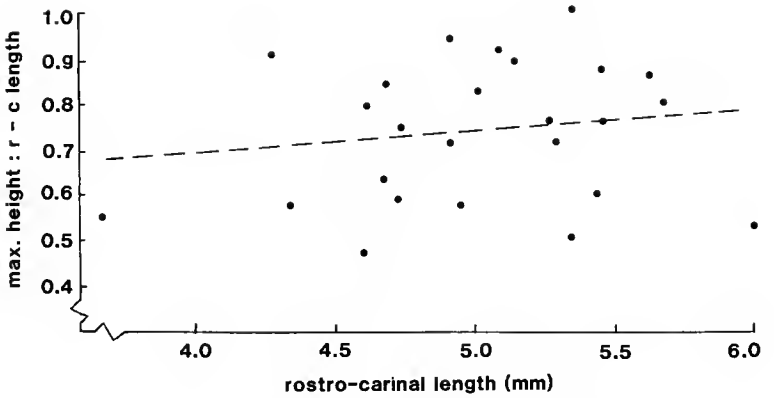

FIG. 11. — Verrucidae: *Verruca trisulcata*, BALGIM, CP92: ratio of maximum shell height to maximum shell width plotted as a function of rostrocarinal length. A ratio of 1.0 is a shell as high as wide; 0.5, half as high as wide. Regression: y = 0.49 + 5.14x, n = 25, R = 0.028, no significant slope.

Verrucidae: Verruca trisulcata, *BALGIM, CP92: rapport de la hauteur maximale de la coquille à sa largeur maximale en fonction de la longueur rostrocarinale. Un rapport de 1,0 correspond à une coquille aussi haute que large ; de 0,5, moitié moins haute que large. Régression : y = 0,49 + 5,14x, n = 25, R = 0,028, pas de pente significative.*

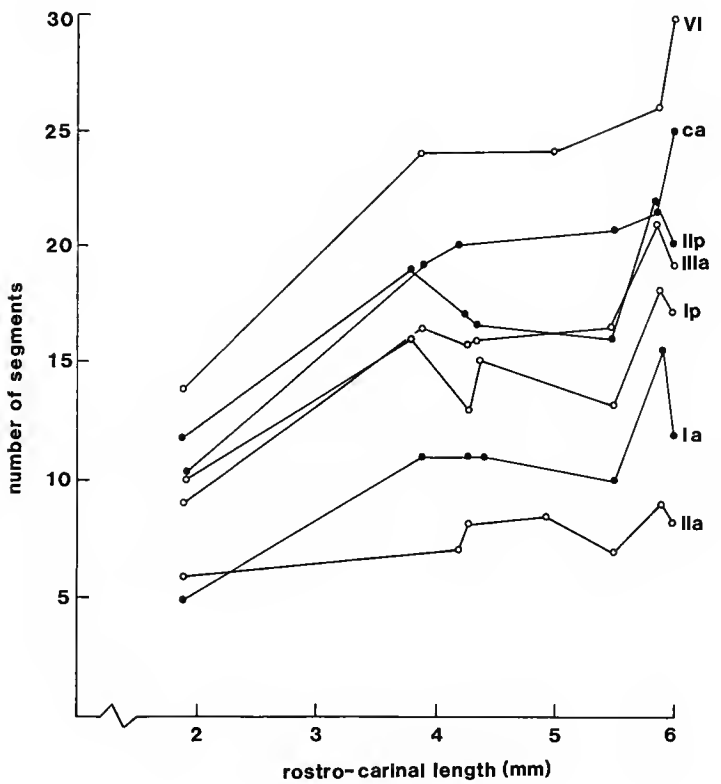

FIG. 12. — Verrucidae: *Verruca trisulcata*, BALGIM, CP92: Mean numbers of segments of rami as a function of size of specimen. For anterior (a) rami of cirri I-III and posterior (p) rami of cirri I and II, and all rami of cirri IV-VI, and caudal appendages (ca).

Verrucidae: Verruca trisulcata, *BALGIM, CP92: Nombres moyens de segments des rames en fonction de la taille des spécimens. Rame antérieure (a) des cirrhes I-III, postérieure (p) des cirrhes I et II, ensemble des rames des cirrhes IV-VI, et appendices caudaux (ca).*

Gruvel, 1920 from off Madeira Is, *V. entobapta* Pilsbry, 1916 from off Florida, and *V. macani* Stubbings, 1936 from off Zanzibar could be the same species.

Altiverruca gibbosa Hoek, 1883
(Fig. 13A, B)

MATERIAL. — BALGIM: CP108, 1527 m (1 empty shell).

RECORDS. — HOEK, 1883: 134, Crozet Is, 1893 m; NILSSON-CANTELL, 1928: 25, Celebes, 3056 m (see for synonymy *sulcata*, *bicornuta*, *mitra*); BROCH, 1931: 45, East Indies, 385 m; ZEVINA, 1971: 439, off Chile, 1230-1700 m; NEWMAN & Ross, 1971: 135, South Georgia, 1098-1153 m; FOSTER, 1981: 352, Kermadec Is and Norfolk I, 590-949 m. As *gibbosa somaliensis* Nilsson-Cantell, 1929: 470, East-African coast, 1079-1289 m. As *bicornuta* Pilsbry 1916: 43, off Nantucket, 3127 m. As *sulcata* Hoek, 1883: 139, off New Zealand, 950-1165 m. As *mitra* Hoek, 1907b, Antarctic Peninsula, 555 m. As *darwini* Pilsbry, 1907a: 111, off Cape May, 2844 m. As *rathburniana* Pilsbry, 1916: 41, off Cape Cod, 3235 m; NILSSON-CANTELL, 1927: 776, Cape Verde Is, 1812 m.

REMARKS

The single empty shell is a dirty yellow colour with clearly delimited growth lines. Basal maximum length (rostrocarinal) 4.5 mm; apical rostrocarinal length (rcl) 5.2 mm; *i.e.* apex of carina flared outward. Tergal height 5.0 mm. The operculum orifice is at an angle of 45 degrees to the base.

A. gibbosa is distinguished from *V. trisulcata* by the ridges and shelf above the superior articular ridge of the rostrum, and from *V. sinuosa* (above) by the very definite sculpturing of the whole shell. A single specimen does not permit any examination of existing or further synonymy, but it does show how a widely distributed, recorded and considered barnacle can be sparsely represented in intensive collecting.

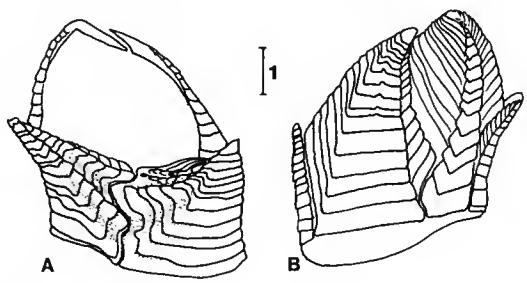

FIG. 13. — Verrucidae: A, B, *Altiverruca gibbosa* BALGIM, CP108, "front" and "rear" views of empty shell. Scale in mm.
Verrucidae: A, B, Altiverruca gibbosa *BALGIM, CP108, vues frontale et postérieure d'une coquille vide. Échelle en mm.*

Altiverruca vertica n.sp.
(Fig. 14)

MATERIAL. — BALGIM: CP92, 1182 m (1 specimen: holotype MNHN Ci 2138).

DESCRIPTION OF HOLOTYPE

3.2 mm umbo rostrocarinal length (rcl): shell higher than wide, with operculum held nearly perpendicular to base. Base calcareous. Carina higher than rostrum; upper margins to movable

opercula continuous and shallowly concave. Rostrum broadly quadrangular; suture with carina without interlocking. All plates lightly sculptured with growth lines. Movable tergum square, and with 2 broad articular ribs above a barely defined diagonal rib. Movable scutum 0.5 times width of tergum, with diagonal rib placed close to articular edge, and internally with a deep muscle pit apically.

Cirrus I with anterior ramus 1 segment longer than posterior ramus. Cirri II and III with anterior rami shorter than posterior rami. Cirri IV-V damaged. Cirrus VI with 25 segments in subequal rami, and intermediate segments with 2 pairs of setae on the anterior edge. Mean segments per rami as follows, anterior ramus first:

I	II	III	IV	V	VI	ca
10,9	7,10	13,16	20,22	–	25,25	7

Caudal appendages 0.5 times length of basal podomere of pedicle of cirrus VI.

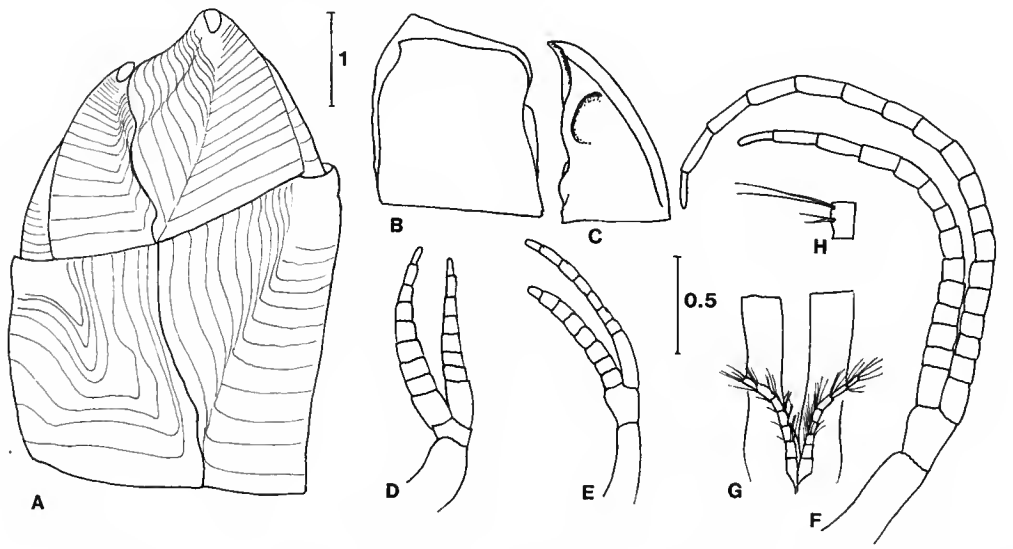

FIG. 14. — Verrucidae: *Altiverruca vertica* sp. nov. Holotype BALGIM, CP92: A, holotype (3.2 mm rcl). B, C, tergum and scutum, inner views. D, cirrus I. E, cirrus II. F, cirrus III. G, pedicles of cirri VI and caudal appendages. H, intermediate segment of cirrus VI. Scales in mm.

Verrucidae : Altiverruca vertica *sp. nov. Holotype BALGIM, CP92 : A, holotype (lrc = 3,2 mm). B, C, tergum et scutum, vues internes. D, cirrhe I. E, cirrhe II. F, cirrhe III. G, partie basale des cirrhes VI et appendices caudaux. H, segment intermédiaire du cirrhe VI. Échelles en mm.*

REMARKS

This species is represented by a solitary specimen. It is similar to *quadrangularis*, being lightly sculptured, smooth surfaced, the operculum held at a steep angle to the base, and the

rostrum and carinal in "front" view broadly quadrangular, but there is no interlocking between rostrum and carina; further, the scutum is much narrower. The specimen is larger than the largest *V. quadrangularis*, and it is notable that the caudal appendages are more diminutive. The shell resembles *V. casula* Hoek, 1913, of Malaysian seas; the appendages of *V. casula* have not been described, and *V. casula* is notable for the broad rostral rib interlocking with the carina.

Metaverruca recta (Aurivillius, 1898)
(Fig. 15)

MATERIAL. — BALGIM: CP92, 1182 m (10 specimens); CP95, 1378 m (9); CP97, 1515 m (2); CP109, 1200 m (1); DW157, 1108 m (1). EPI I: CP38 (Celtic Sea), 2100 m (1).

RECORDS. — AURIVILLIUS, 1898: 195 and GRUVEL, 1920: 46, Azores, 861-1385 m; SOUTHWARD & SOUTHWARD, 1958: 637, Bay of Biscay, 329-1774 m. As *sculpta* Aurivillius, 1898: 197 and GRUVEL, 1920: 41, Azores, 454 m; NILSSON-CANTELL, 1929: 461, Scotland, 1326 m; BROCH, 1931: 41, Kei Is, 345 m; FOSTER, 1981: 352, Kermadec Is, 501-1180 m. As *magna* Gruvel, 1901: 261; 1902: 109, Gulf of Gascogne, 1480 m; GRUVEL, 1920: 50. As *linearis* Gruvel, 1900b: 243 and GRUVEL, 1902: 107, Azores, 960-2018 m. As *halotheca* Pilsbry, 1907b: 188, Hawaii, 1670 m; Pilsbry, 1916: 46, Hawaii, 417-430 m; FOSTER, 1978: 69, New Zealand, 252-896 m. As *capsula* Hoek, 1913: 130, East Indies, 520-1301 m; STUBBINGS, 1936: 38, Zanzibar, 333 m. As *coraliophila* Pilsbry, 1916: 21, Florida — Bahamas, 506-794 m. As *sculpta* Buckeridge, 1983: 59; Miocene of New Zealand; BUCKERIDGE, 1994: 116 (for full synoymy); FOSTER & BUCKERIDGE, 1994: 368, La Réunion, 620-1230 m.

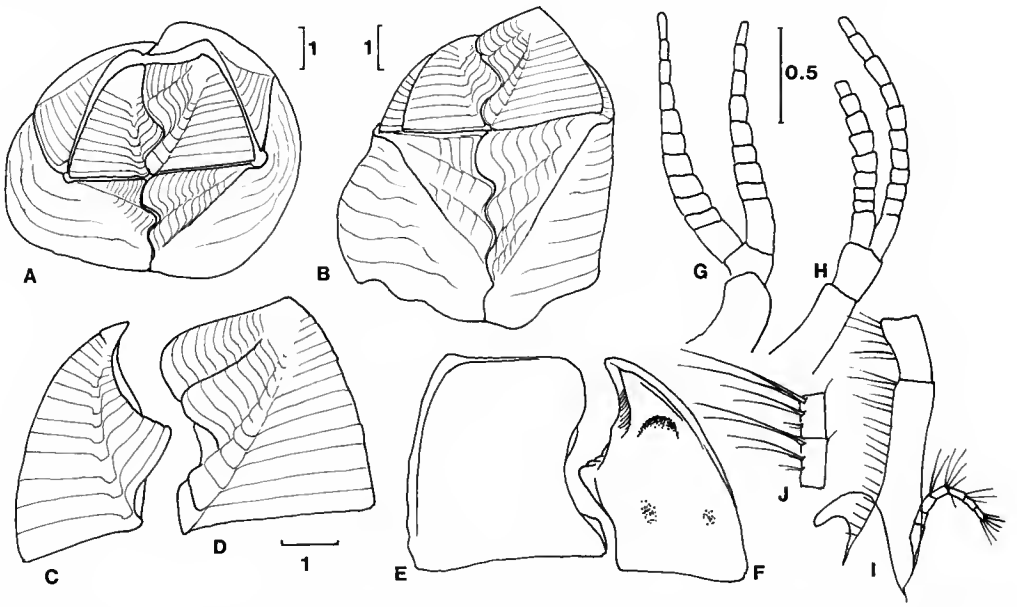

FIG. 15. — Verrucidae: *Metaverruca recta*, A, top view (4.5 mm rcl) BALGIM, CP95. B, oblique view (5.1 mm rcl) BALGIM, CP92. C, D, outer views scutum and tergum (of 5.1 mm rcl specimen) BALGIM, CP92. E, F, inner views, *ditto*. G, cirrus I; H, cirrus II; I, pedicle cirrus VI, penis and caudal appendages; J, intermediate segments cirrus VI; all of 5.0 mm rcl specimen, BALGIM, CP95, and all to same scale. Scales in mm.

Verrucidae : Metaverruca recta, *A, vue de dessus (lrc = 4,5 mm) BALGIM, CP95. B, vue oblique (Rcl = 5,1 mm) BALGIM, CP92. C, D, vues externes du scutum et du tergum (spécimen ayant une lrc de 5,1 mm) BALGIM, CP92. E, F, vues internes,* dito. *G, cirrhe I ; H, cirrhe II ; I, partie basale du cirrhe VI, pénis et appendices caudaux ; J, segments intermédiaires du cirrhe VI ; provenant tous d'un spécimen ayant une lrc de 5,0 mm, BALGIM, CP95, et tous à la même échelle. Échelles en mm.*

REMARKS

Accepting the synonymies, this is a widespread barnacle, from North Atlantic through Indian to North and South Pacific Oceans. It is characterised by its particularly compact form, more roundly sessile than narrowly erect like *V. quadrangularis*, with the apeces of the rostrum and tergum set in from the basal margin (*i.e.* the shell is conical rather than splayed), with the upper ribs between the rostrum and carina very wide, mostly 2, sometimes 3 of them; by the edge of articulation of the movable plates forming a straight line between the apeces of the rostrum and carina; by the general D-shape of the orifice; by the operculum being held at an angle 45-90 degrees to the perpendicular depending on the nature of the substratum; by the myophores; and by the generally large size of grown specimens for the genus (8-10 mm basal length). The appendages have been described by FOSTER (1978) and BUCKERIDGE (1994); notable is the shortness of the caudal appendages.

Mean numbers of segments in cirri of 4 specimens (CP95) as follows, anterior ramus first:

rcl (mm)	I	II	III	IV	V	VI	ca
1.0	6,5	5,6	8,10	15,17	16,14	14,17	5
1.3	7,6	5,7	9,12	15,16	19,19	21,21	5
2.9	12,9	8,11	18,21	22,26	26,28	30,31	7
4.3	12,10	8,12	19,20	20,21	23,22	20,21	7

Family PACHYLASMATIDAE Buckeridge, 1983

Pachylasma giganteum (Philippi, 1836)
(Fig. 16A, B)

MATERIAL. — BALGIM: DR37, 864 m (3 shells); DR40, 362 m (75 specimens, 14-34 mm basal diameter); DR49, 521 m (1 specimen); DR111, 285 m (6 specimens); DR115, 352 m (1 shell); DW116, 340 m, (1 shell); DR152, 550 m (1 shell); DR153, 580 m (99 specimens, 6-47 mm basal diameter).

RECORDS. — DARWIN, 1854: 477, Mediterranean; PILSBRY, 1916: 329, Strait of Messina; STUBBINGS, 1967: 263, off West Africa; WELTNER, 1897: 273, Mediterranean, on *Errina aspera*; RELINI, 1980: 49, Italy, 150-200 m. See NEWMAN & ROSS (1976: 40) for full synonymy; distribution quoted as "Mediterranean – West Coast Africa".

REMARKS

This barnacle is well described by DARWIN (1854), who quoted a maximum size of 29.2 mm basal rostrocarinal length. Very small specimens have no carinolatera. Few of the records of this barnacle give depth data. The present records are precise, 285-864 m, just west of the Straits of Gibraltar. Four of the stations yielded only shells (easily recognised by their thickness and the irregular basal edges) and 2 of the stations yielded rock substratum with large numbers of specimens growing on it and themselves.

Family BATHYLASMATIDAE Newman & Ross, 1971

Bathylasma hirsutum (Hoek, 1883)
(Fig. 16C, D)

MATERIAL. — BALGIM: CP36, 990 m (1 shell only); DR37, 864 m (72 shells).

RECORDS. — See NEWMAN & ROSS (1976: 46) for full references, and distribution "Northeast Atlantic from Faroe Is to Azores, 944-1829 m". SOUTHWARD & SOUTHWARD (1958) give a useful list of collecting data, including depth range of 384-1829 m.

REMARKS

These 2 stations are a little further south than the stations listed by SOUTHWARD & SOUTHWARD (1958) but do not constitute a significant addition to the known distribution. The large number of shell plates at Stn DR37 (Bay of Cadiz) is quite reminiscent of similar collections of plates of *B. corolliforme* from the Southern Ocean (NEWMAN & ROSS, 1971) and of *B. alearum* from New Zealand (FOSTER, 1978). Evidently, the shell plates of deep water bathylasmatids accumulate in-situ in proximity to appropriate attachment substrata, and in themselves provide substrata for further recruitment and accumulation.

Family BALANIDAE Leach, 1817

Megabalanus tulipiformis (Ellis, 1758)
(Fig. 16E, F)

MATERIAL. — BALGIM: DR40, 362 m (4 shells); DR115, 352 m (1 shell plate); DR133, 195 m (1 specimen).

DISTRIBUTION. — Mediterranean, east Atlantic of France to Cape Verde Is, 25-250 m (NEWMAN & ROSS, 1976: 69; RELINI, 1980: 53).

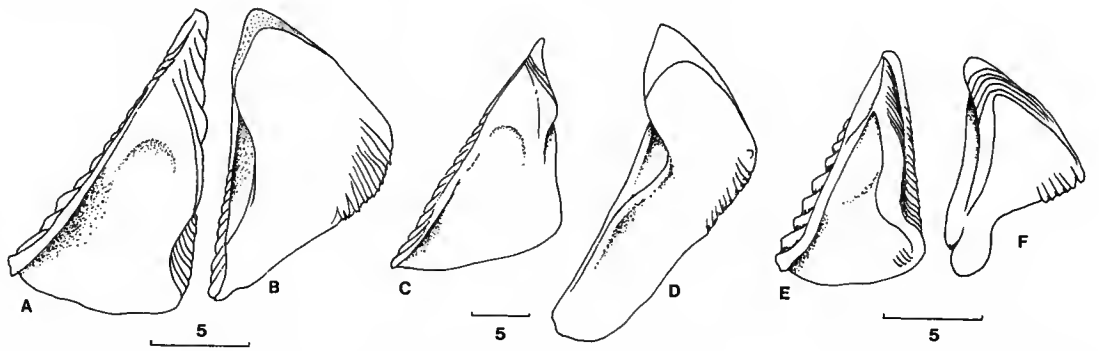

FIG. 16. — Balanomorpha, inner views of opercula: A, B, *Pachylasma giganteum*, scutum and tergum, same individual, BALGIM, DR40. C, D, *Bathylasma hirsutum*, ditto, different individuals, BALGIM, DR37. E, F, *Megabalanus tulipiformis*, *ditto*, same individual, BALGIM, DR133. Scales in mm.

Balanomorpha, opercule, vues internes : A, B, Pachylasma giganteum, *scutum et tergum d'un même individu, BALGIM, DR40. C, D,* Bathylasma hirsutum, dito, *provenant de divers individus, BALGIM, DR37. E, F,* Megabalanus tulipiformis, dito, *d'un même individu, BALGIM, DR133. Échelles en mm.*

REMARKS

Previous authors have noted the occurrence of *M. tulipiformis* with *Pachylasma giganteum*. The single shell plate recovered from station DR115 together with *P. giganteum* was readily identified by its rose pink colour. In the BALGIM collections, *M. tulipiformis* is the only barnacle recovered from any station in the Mediterranean (DR133), and it was the only live material of this species.

BIOGEOGRAPHY

Summary data are presented in Table 1, which gives the number of stations, number of individuals and depth data from these collections and from the literature, for each of the species. Full station data are given in Appendix A.

The frequency of recovery of barnacles in the deep sea grabs and dredges is 23% (29 of 126 stations) for the BALGIM cruise, yielding 882 specimens (14 species).

The North Atlantic Ocean stations (29 BALGIM plus 9 others) provided 20 species, including 2 new to science (*Arcoscalpellum crenulatum* and *Verum frillosum*).

There are 5 species common to New Zealand and the North Atlantic (*Poecilasma kaempferi*, *Smilium acutum*, *Verum novaezelandiae*, *Altiverruca gibbosa* and *Metaverruca recta*). These seem to be part of a circumglobal, or at least North Atlantic to South-West Pacific barnacle fauna, in moderately deep water (1000-2000 m).

Whether deeper sea (> 3000 m) species such as *Trianguloscalpellum gigas*, *T. regium*, *Arcoscalpellum michelottianum* and *Meroscalpellum bifurcatum* are widespread is hard to ascertain from published records, but considering the more limited sampling from such depths they are likely to be so.

The more commonly collected species (*i.e.*, 100 specimens) are: *A. michelottianum*, taken at 11 stations (121 specimens), *Verruca trisulcata*, at 10 stations (400 specimens), and *Pachylasma giganteum*, at 4 stations (181 specimens). The last of these, the shallowest occurring, is most likely restricted to the northern Atlantic Ocean and the Mediterranean Sea. The predominance of records from the North Atlantic, possibly reflects a longer history of collecting there. Biogeographic restrictions are likely to apply to other shallower sea species, (*e.g.*, for the North Atlantic *Scalpellum scalpellum*, *Ornatoscalpellum stroemii*, *Bathylasma hirsutum* and *Megabalanus tulipiformis*), as they are to littoral species.

With respect to a principal aim of the BALGIM cruise, namely to relate Mediterranean outflow water to its deflection to the northern side of the Ibero-Moroccan Bay, it is noteworthy that stations that have *Bathylasma hirsutum*, *Pachylasma giganteum* or *Megabalanus tulipiformis*, do not have verrucomorphs or lepadomorphs. Only one of these stations is in the Mediterranean Sea (DR133, which has *M. tulipiformis* only, and is the only station there to provide barnacles), two are on the sill of the Straits of Gibraltar (DR152 and DR153, with *P. giganteum* only), five are grouped just due west of the sill (DR40, DR49, DR111, DR115 and DW116, with both *M. tulipiformis* and *P. giganteum*), and two further northwest (CP36 and DR37, both with *P. giganteum* and *B. hirsutum*). The Mediterranean barnacle fauna does not have the deep ocean scalpellids and verrucids. The last 9 quoted stations are different from the other Atlantic stations, and could represent a Mediterranean influence.

TABLE 1. — Summary data on numbers of stations, individuals and depths for each of the species.

Species	No of stations	Indiv. sample numbers	Total no	Depth range (m)	
				this paper	literature
Octolasmis niestraszi	1	1	1	80	16-135
Poecilasma kaempferi	1	1	1	1108	126-1885
Smilium acutum	8	1 3 23 45 1 1 3	41	355-2170	61-2480
Trianguloscalpellum regium	2	22 1	23	3100-3380	845-5212
Trianguloscalpellum gigas	1	3	3	3815	3749
Arcoscalpellum michelottianum	11	14 3 27 5 10 2 15 25 9 10 1	121	1182-2160	64-3422
Arcoscalpellum crenulatum n. sp.	1	2	2	3100	—
Amigdoscalpellum praeceps	2	1 1	2	3100-4720	411-2940
Verum ? minutum	3	13 3 3	19	1870-2077	802-3520
Meroscalpellum bifurcatum	2	1 1	2	46613-4720	4151
Verum novaezelaniae	4	1 14 7 1	23	1592-2100	455-2500
Verum frillosum n. sp.	1	1 3	1	3380	—
Ornatoscalpellum stroemii	1		3	355	160-629
Scalpellum scalpellum	1	21	21	347	50-400
Verruca tricsulcata	7	9 4 70 252 28 9 22	394	890-1378	441-1690
Altiverruca gibbosa	1	(1)	(1)	1527	555-1289
Altiverruca vertica n. sp.	1	1	1	1182	—
Metaverruca recta	6	10 9 2 1 1 1	24	1108-2100	329-2110
Pachylasma giganteum	8	(3) 75 1 6 (1) (3) 75 1 6 (1) (1) (1) 99	187	285-864	150-250
Bathyslama hirsutum	2	(1) (72)	73	864-990	944-1829
Megabalanus tulipiformis	3	(4) (1) 1	6	135-195	

Acknowledgements

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APPENDIX A. — Cruise and station data, and barnacles and numbers of barnacles collected at each station.

ATLANTIC OCEAN

BALGIM. — A study to correlate composition of benthic fauna and origin of water masses between the Atlantic Ocean and Mediterranean Sea. This material was collected May-June 1984 aboard R.V. "Cryos" during cruise BALGIM, conducted for Centre national de la recherche scientifique (PIROCEAN), under the direction of Dr P. BOUCHET (Museum). Dates: 29.5.84-18.6.84.

Stn	m	°N	°W	Species	#
CP10	1592	36.453	9.320	*Arcoscalpellum michelottianum*	14
				Verum novaezelandiae	1
CP17	1470	36.453	9.308	*Arcoscalpellum michelottianum*	3
CP36	990	36.166	7.137	*Bathylasma hirsutum*	(1)
DR37	864	36.178	7.154	*Pachylasma giganteum*	(3)
				Bathylasma hirsutum	(72)
DR40	362	35.499	6.086	*Pachylasma giganteum*	75
				Megabalanus tulipiformis	(4)
DR49	521	35.530	6.328	*Pachylasma giganteum*	1
CP63	1510	35.306	7.421	*Arcoscalpellum michelottianum*	27
CP65	1805	35.265	7.599	*Smilium acutum*	1
				Arcoscalpellum michelottianum	5
CP68	2035	35.119	7.526	*Smilium acutum*	3
				Arcoscalpellum michelottianum	10
				Verum ? minutum	13
CP69	2028	35.114	7.505	*Smilium acutum*	23
				Arcoscalpellum michelottianum	2
				Verum ? minutum	3
DR82	355	33.455	8.320	*Smilium acutum*	4
				Ornatoscalpellum stroemii	3
CP90	890	34.214	7.236	*Verruca trisulcata*	9
CP91	948	34.223	7.251	*Verruca trisulcata*	4
CP92	1182	34.243	7.303	*Arcoscalpellum michelottianum*	15
				Verruca trisulcata	70
				Altiverruca vertica	1
				Metaverruca recta	10
CP95	1378	34.240	7.393	*Arcoscalpellum michelottianum*	25
				Verruca trisulcata	22
				Metaverruca recta	9

CP97	1515	34.254	7.411	*Arcoscalpellum michelottianum*	9
				Metaverruca recta	2
CP99	1870	34.282	7.433	*Arcoscalpellum michelottianum*	10
				Verum ? minutum	3
CP103	347	34.107	7.298	*Scalpellum scalpellum*	21
CP108	1527	36.108	8.062	*Altiverruca gibbosa*	(1)
CP109	1200	36.145	7.564	*Metaverruca recta*	1
DR111	285	35.569	6.221	*Pachylasma giganteum*	6
DR115	332	35.475	6.042	*Pachylasma giganteum*	(1)
				Megabalanus tulipiformis	(1)
DW116	340	35.486	6.042	*Pachylasma giganteum*	(1)
DR133	195	35.258	4.174	*Megabalanus tulipiformis*	(1)
DR152	550	35.567	5.347	*Pachylasma giganteum*	(1)
DR153	580	35.558	5.353	*Pachylasma giganteum*	99
CP156	1135	36.200	7.527	*Poecilasma kaempferi*	1
				Verruca trisulcata	252
DW157	1108	36.210	7.558	*Poecilasma kaempferi*	1
				Verruca trisulcata	28
				Metaverruca recta	1
CP160	1350	36.146	8.009	*Verruca trisulcata*	9

BAY OF BISCAY. — This material was collected during missions organised by IFREMER (Brest) between 1974 and 1987.

BIOGAS V					
CP07	2170	44.098	4.164	*Smilium acutum*	5
BIOGAS VII					
CP28	3380	47.295	9.035	*Trianguloscalpellum regium*	2
				Scalpellum frilloswn	1
BIOGAS VIII					
CP30	3100	47.296	9.061	*Verum regium*	21
				Arcoscalpellum crenulatum	2
				Amigdoscalpellum praeceps	1
BIOGAS XI					
CP35	4720	46.343	10.230	*Arcoscalpellum praeceps*	1
				Meroscalpellum bifurcatum	1
EPI I					
CP38	2100	47.338	8.422	*Smilium acutum*	1
				Verum novaezelandiae	14
				Metaverruca recta	1
CP39	2100	47.320	8.384	*Verum novaezelandiae*	7
				Smilium acutum	1

EPI VI					
KG229	2160	47.270	8.320	*Arcoscalpellum michelottianum*	1

GASCOR. — This material was collected during mission GASCOR, from deep-sea modules placed by EPI (Environnement Profond: Impact), organised by IFREMER, Brest; chief, Gerard AUFFRET. Date: 16.3.86.

CP42	3815	46.227	12.368	*Trianguloscalpellum gigas*	3

BIOCYAN. — This material was collected during mission BIOCYAN 2, with submersible CYANA, organised by Centre océanologique de Bretagne (COB, Brest); chief, Myriam SIBUET. Date: 26.6.83.

PL18	2000	47.321	8.276	*Smilium acutum*	3

WALDA. — This material was collected during mission WALDA, organised by Centre océanologique de Bretagne (COB, Brest). Collected off Angola. Date: 23.6.71.

		°S	°E		
CY09	4613	19.103	9.181	*Meroscalpellum bifurcatum*	1

SOUTH-WEST PACIFIC

CORINDON II. — This material was collected during the cruise CORINDON II, organised by ORSTOM: Responsible for biological data. Jacques FOREST (Museum). Dates: 29.10.80-12.11.80. Straits of Makassar, 15-2 400 m.

236	1730	0.067N	119.455	*Verum novaezelandiae*	1
248	170	0.542S	119.287	scalpellid juvenile indet.	
263	80	1.568S	119.167	*Octolasmis nierstraszi*	1

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n° 1-2 : 193-200.

A new species of *Didymochelia* from New Caledonia (Crustacea: Amphipoda: Didymocheliidae)

by Jim K. LOWRY & Helen E. STODDART

Abstract. — Didymocheliid amphipods are extremely rare. *Didymochelia ledoyeri* sp. nov. is described from New Caledonian material. It is only the fourth specimen collected and the third species described. This is the first record of the family outside the subantarctic area.

Keywords. — Amphipoda, Didymocheliidae, taxonomy, new species, New Caledonia.

Une espèce nouvelle de *Didymochelia* de Nouvelle-Calédonie (Crustacea : Amphipoda : Didymocheliidae)

Résumé. — Les amphipodes didymocheliides sont extrêmement rares. *Didymochelia ledoyeri* sp. nov. de Nouvelle-Calédonie est seulement le quatrième spécimen capturé et la troisième espèce décrite. La famille est signalée pour la première fois en dehors de la zone subantarctique.

Mots-clés. — Amphipoda, Didymocheliidae, taxonomie, espèces nouvelles, Nouvelle-Calédonie.

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INTRODUCTION

The didymocheliids are among the rarest amphipods known. K. H. BARNARD (1931) first described *Didymochelia spongicola* from one specimen living among sponges at South Georgia. He was not able to place it in a family and the species has not been collected since. BELLAN-SANTINI & LEDOYER (1987) described the second species, *D. edwardi*, based on two specimens from Prince Edward Island. They established a new family, Didymocheliidae, and compared it to the Lysianassidae and the Acanthonotozomatidae. They considered the family to have closest affinities with the Lysianassidae.

A fourth specimen of *Didymochelia* has been discovered among recent MUSORSTOM collections from New Caledonia and is described here as *Didymochelia ledoyeri* sp. nov. The unique specimen is lodged in the Muséum national d'Histoire naturelle, Paris (MNHN).

In this paper we change the terminology we have previously used to describe setae and spines. This change is based primarily on arguments about the homology of setae and spines presented by OSHEL & STEELE, 1988, and WATLING, 1989. The terminology mainly follows WATLING, 1989, with a few modifications. What we have previously referred to as setae are now referred to as slender setae and what we previously referred to as spines are now called robust setae. What we previously referred to mainly as teeth (non-articulating extrusions of the cuticle), are now referred to as spines.

The following abbreviations are used on the plates : **A**, antenna; **G**, gnathopod; **MD**, mandible; **MP**, maxilliped; **MX**, maxilla; **P**, peraeopod; **T**, telson; **U**, uropod; **l**, left; **r**, right.

Didymochelia K. H. Barnard, 1931

Didymochelia K. H. Barnard, 1931 : 429. – K. H. Barnard, 1932 : 247. – Bellan-Santini & Ledoyer, 1987 : 367. – Barnard & Karaman, 1991 : 276.

Didymocheila J. L. Barnard, 1969 : 478 (*lapsus calami*).

Key to the species of *Didymochelia*

1. Pleonite 3 with dorsodistal boss; coxa 7 with produced acute posterodistal corner 2
— Pleonite 3 without dorsodistal boss; coxa 7 with non-produced subquadrate posterodistal corner ..... *D. ledoyeri* sp. nov.
2. Pleonite 3 with rounded dorsodistal boss ..... *D. edwardi* Bellan-Santini & Ledoyer
— Pleonite 3 with recurved acute boss ..... *D. spongicola* K. H. Barnard

Didymochelia ledoyeri sp. nov.
(Figs 1-3)

Type material. — Loyalty Basin east of Thio, New Caledonia, 21° 28' S 166° 21.5' E, depth 700-1265 m, collected from deep-sea submersible, *Cyana*, 3 March 1989, H. Zibrowius, CALSUB : stn PL 12 : 1 ♂, holotype, 4.5 mm (MNHN-Am 4484).

Etymology. — This species is named in recognition of the contribution of Michel Ledoyer to amphipod systematics.

Distribution. — *Didymochelia ledoyeri* is known only from New Caledonia in 700 to 1265 m depth.

Diagnosis

Peraeopod 4 : coxa without posteroventral lobe. Peraeopod 6 : coxa with rounded posteroventral corner. Peraeopod 7 : coxa with subquadrate posteroventral corner. Pleonite 3 without dorsal boss. Epimera 2-3 with tiny posteroventral tooth.

Description

Based on holotype male, female not known. Head and body : without setae, colour not known. *Head* : exposed, deeper than long; lateral cephalic lobe large, broadly rounded; rostrum absent; eyes apparently absent. *Antenna 1* : medium length, 0.23 × body; peduncular article 1 short, length 1 × breadth, distal margin with small midmedial swelling; peduncular article 2 short, 0.4 × article 1; peduncular article 3 short, 0.13 × article 1; accessory flagellum long, about 0.5 × primary flagellum, at least 3-articulate, article 1 long, 1.25 × article 2; flagellum 5-articulate; callynophore strong 2-field, without posterodistal setae or robust setae, without flagellar robust setae, calceoli absent. *Antenna 2* : slightly longer than antenna 1; peduncle without brush setae; flagellum 7-articulate, calceoli absent.

Mouthpart bundle : conical. *Epistome* and *upper lip* : fused. *Mandible* : incisors serrate, each with about 7 cusps; left and right laciniae mobilis present, left, a broad serrate blade, right, a distally cuspidate peg; accessory setal row with simple robust setae distally and distally cuspidate

pegs proximally; with pappose intermediate setae; molar columnar with weakly triturating surface, with large plumose seta on each molar; mandibular palp attached slightly proximally; article 1 short, length 1 × breadth, without setae; article 2 elongate, slightly broadened proximally, length 2.7 × breadth, 1.5 × article 3, with 7 posterodistal A2-setae; article 3 slender, blade-like, short, length 2.5 × breadth, with 4 (left), 5 (right) distal D3-setae, and 2 apical E3-setae.

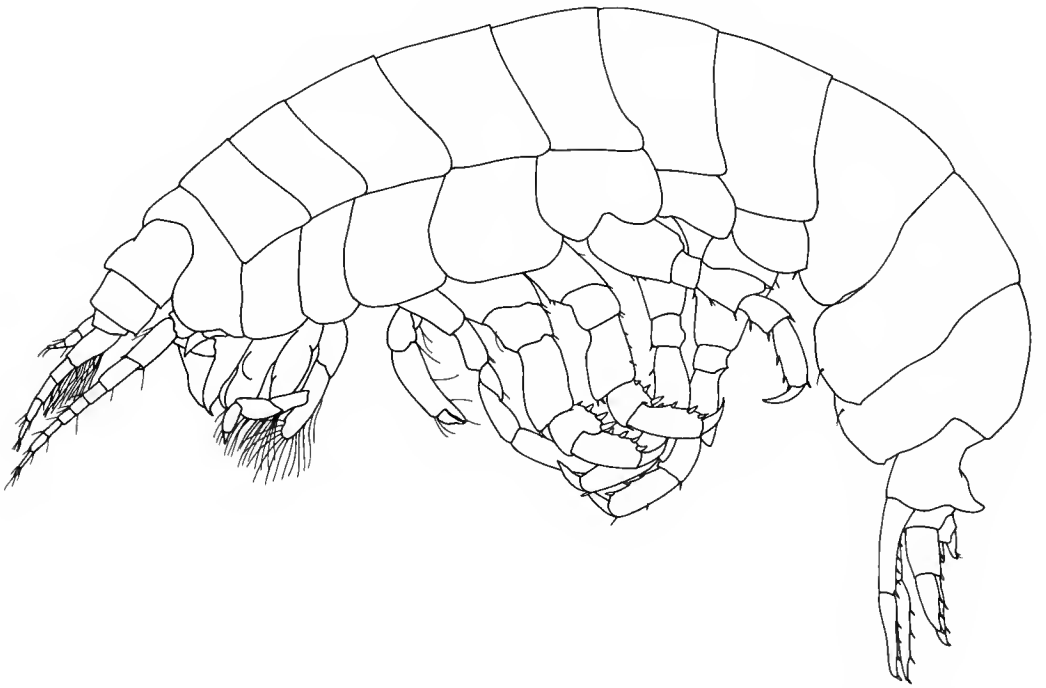

FIG. 1. — *Didymochelia ledoyeri* sp. nov., holotype male, 4.5 mm, MNHN-Am 4484, Loyalty Basin, New Caledonia.
Didymochelia ledoyeri *sp. nov., holotype, mâle 4,5 mm, MNHN-Am 4484, bassin des Loyautés, Nouvelle-Calédonie.*

Maxilla 1 : inner plate tapering distally, inner margin fully setose, 19 plumose setae; outer plate narrow with 9 long, slender multicuspidate setal-teeth; palp large, 2-articulate, with 13 long, plumose terminal setae. *Maxilla 2* : inner and outer plates broad, inner plate 0.9 × length outer plate, with well developed oblique setal row. *Maxilliped* : inner plate large, subquadrate, long plumose setae line apical and medial margins; outer plate small, subovate, with long, plumose apical, medial and submarginal setae; palp 4-articulate, article 2 slender, length 2.1 × breadth, subequal in length to article 3, article 3 long, slender, length 2.7 × breadth; dactylus well developed, unguis present (right dactylus damaged).

Peraeonites : 1 to 7 dorsally smooth. *Gnathopod 1* : chelate; coxa large, as long as coxa 2, anterior and posterior margins straight; basis long, slender, length 3.2 × breadth, anterior

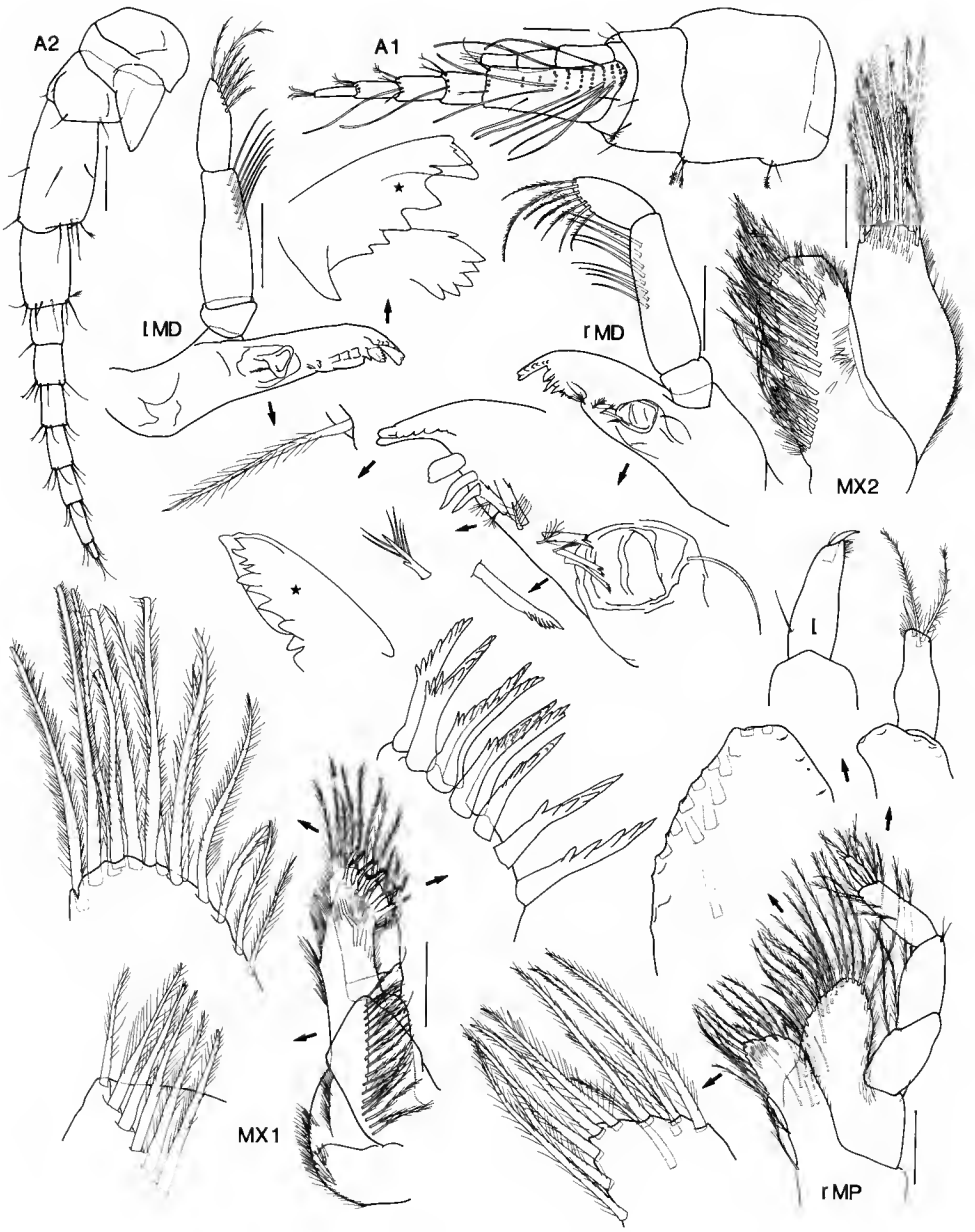

FIG. 2. — *Didymochelia ledoyeri* sp. nov., holotype male, 4.5 mm, MNHN-Am 4484, Loyalty Basin, New Caledonia. * Drawn from new moult. Scales represent 0.1 mm.

Didymochelia ledoyeri *sp. nov., holotype, mâle 4,5 mm, MNHN-Am 4484, bassin des Loyautés, Nouvelle-Calédonie. * Dessiné d'après une exuvie. Échelles = 0,1 mm.*

margin with 1 proximal simple seta; ischium short, length 1.3 × breadth; merus, posterior margin with a few simple setae; carpus subtriangular, short, length 1.3 × breadth, shorter than (0.5 ×) propodus; propodus large, subrectangular, length 2.3 × breadth, margins subparallel, posterior margin smooth, slightly concave, with a few plumose setae and very fine setae near posterior margin; palm extremely obtuse, margin straight, smooth, posterior corner without robust setae; dactylus simple. *Gnathopod 2*: chelate; coxa large, subequal in size to coxa 3; ischium short, length 1.7 × breadth; carpus subrectangular, long, length 2.6 × breadth, subequal in length to propodus; propodus large, subrectangular, length 2.7 × breadth, margins subparallel, posterior margin smooth, straight, with a few plumose setae and very fine setae near posterior margin; palm extremely obtuse, margin straight, smooth, posterior corner without robust setae; dactylus simple.

Peraeopods 3 and 4: coxa large, anterior margin straight with broadly rounded anteroventral corner, posterior margin straight; merus weakly expanded anteriorly with short robust setae along posterior margin; carpus short, broader than long, with short robust setae along posterior margin; propodus twice as long as broad, with 3-4 short robust setae and 2 distal locking setae along posterior margin; dactylus short, slender, with well developed unguis. *Peraeopod 5*: coxa bilobate, anterior lobe slightly produced; basis slightly expanded posteriorly with slightly rounded, smooth posterior margin; merus slightly expanded posterodistally with 2 distal robust setae; propodus with 2 robust setae and 2 distal locking setae along anterior margin; dactylus short, slender, with well developed unguis. *Peraeopod 6*: coxa small, slightly lobate posteriorly; basis slightly expanded posteriorly with straight, smooth posterior margin; merus slightly expanded posterodistally with 1 distal seta; propodus with 2 robust setae and 2 distal locking setae along anterior margin; dactylus short, slender, with well developed unguis. *Peraeopod 7*: coxa small, not lobate posteriorly; basis slightly expanded with sinusoidal, smooth posterior margin; merus slightly expanded posterodistally with 1 marginal robust seta and 3 distal robust setae; propodus with 2 robust setae and 2 distal locking setae along anterior margin; dactylus short, slender, with well developed unguis.

Gills: from gnathopod 2 to peraeopod 7, simple, small; gill on peraeopod 7 very small.

Pleonites 1 to 3: dorsally smooth. *Epimeron 1*: posteroventral corner rounded. *Epimeron 2* : posteroventral corner with tiny tooth. *Epimeron 3*: posteroventral corner with tiny tooth. *Urosomite 1*: large with well developed, subacute dorsal boss. *Urosomites 2 and 3*: very small. *Uropod 1*: peduncle with 4 dorsolateral, 1 apicolateral and 2 dorsomedial robust setae; rami subequal in length; outer ramus with 4 lateral robust setae; inner ramus with 1 medial and 2 lateral robust setae. *Uropod 2*: peduncle with 1 dorsolateral and 1 apicolateral robust setae; rami subequal in length; outer ramus with 2 lateral robust setae; inner ramus with 2 medial and 3 lateral robust setae. *Uropod 3*: peduncle short, with 1 slender seta; rami absent. *Telson*: length 0.75 × breadth, entire, distal margin truncated, with 2 pairs of subterminal penicillate setae and 2 short, terminal robust setae.

Remarks

Didymochelia spongicola K. H. Barnard, 1931 and *D. edwardi* Bellan-Santini & Ledoyer, 1987, are very similar. *Didymochelia ledoyeri* differs from both of these species in coxa 4 which has no posteroventral lobe, coxae 6 and 7 which are not produced and epimera 2-3, both of which have a tiny posteroventral tooth.

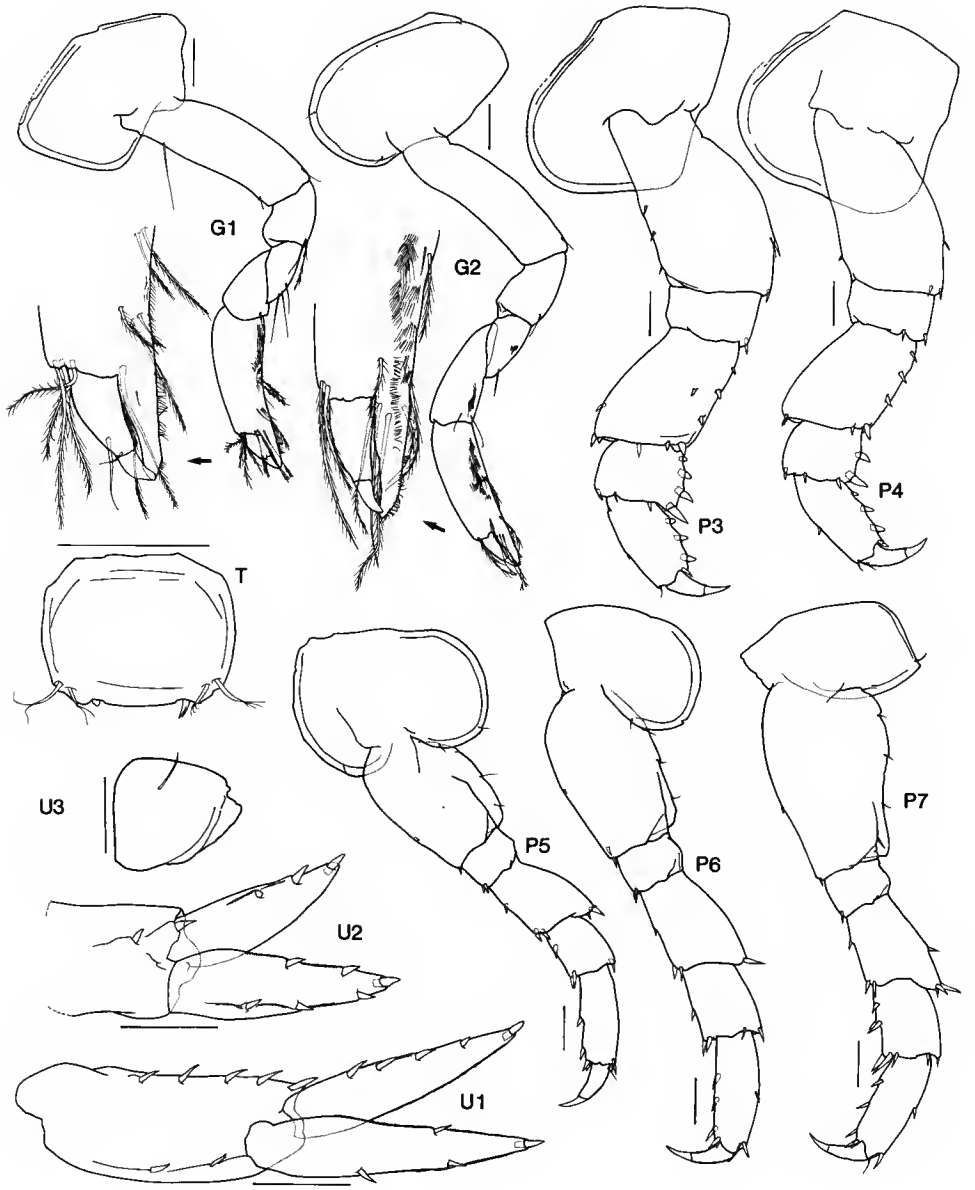

FIG. 3. — *Didymochelia ledoyeri* sp. nov., holotype male, 4.5 mm, MNHN-Am 4484, Loyalty Basin, New Caledonia. Scales represent 0.1 mm.

Didymochelia ledoyeri *sp. nov., holotype, male 4,5 mm, MNHN-Am 4484, bossin des Loyoutés, Nouvelle-Calédonie. Échelles = 0,1 mm.*

Acknowledgements

We are particularly grateful to Alain CROSNIER who originally encouraged us to study the amphipods from the MUSORSTOM Expeditions and who arranged for one of us to come to Paris and sort the collections. We thank the Australian Museum Trust who provided travel money for this project. We thank Stephen KEABLE who illustrated the species and Roger SPRINGTHORPE who composed and inked the plates.

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n° 1-2 : 201-210.

Two new species of *Nanocassiope* from the Western Pacific (Crustacea, Brachyura, Xanthidae)

by Peter J. F. DAVIE

Abstract. — Two new species of *Nanocassiope* Guinot, 1967, are described, *N. oblonga* from French Polynesia, and *N. tridentata* from Indonesia. This brings to six the number of species attributed to the genus, with four found in the Indo-West Pacific region.

Keywords. — Crustacea, Decapoda, Brachyura, Xanthidae, *Nanocassiope*, Pacific, Indonesia, French Polynesia, new species.

Deux nouvelles espèces de *Nanocassiope* de l'Indo-Pacifique (Crustacea, Brachyura, Xanthidae)

Résumé. — Deux nouvelles espèces de *Nanocassiope* Guinot, 1967 sont décrites : *N. oblonga* de Polynésie française et *N. tridentata* d'Indonésie. Six espèces sont donc attribuées à ce genre dont quatre ont été récoltées dans l'Indo-Pacifique occidental.

Mots-clés. — Crustacea, Decapoda, Brachyura, Xanthidae, *Nanocassiope*, Pacifique, Indonésie, Polynésie française, espèce nouvelle.

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INTRODUCTION

The present study was initiated by the discovery of what appeared to be a new *Nanocassiope* Guinot, 1967, species amongst xanthid crab collections made by J. POUPIN of the French Service Mixte de Contrôle Biologique (SMCB). The collections were made from the F. R. V. *Marara* which conducted biological surveying throughout French Polynesia. The present specimens of this new species were collected by dredge on the outer slopes of the islands in depths ranging from 100 to 200 m. Deep water xanthid species collected from this region by trapping have been previously reported by Davie (1993).

While examining comparative specimens held at the MNHN, a single male specimen of a further new species was discovered that had been collected by the Rumphius I Expedition from the vicinity of Ambon, Indonesia (see ROMIMOHTARTO, 1974). The opportunity was therefore taken to describe both species at the same time.

Abbreviations used in the text are: mm, millimetres; G1, G2, first and second male gonopods; MNHN, Muséum national d'Histoire naturelle, Paris; QM, Queensland Museum, Brisbane. The

abbreviated terminology used for carapace regions is that used by SERÈNE (1984) following DANA (1852). Measurements given in the text are of carapace breadth (c.b.) followed by length.

Family XANTHIDAE MacLeay, 1838
XANTHINAE MacLeay, 1838

Nanocassiope Guinot, 1967

Nanocassiope Guinot, 1967: 355-358; 1971: 1075. – SAKAI, 1976: 433. – SERÈNE, 1984: 209.

DIAGNOSIS

Carapace broad, moderately convex, distinctly areolated with the protogastric, mesogastric and hepatic regions, and epigastric lobes, separated by distinct grooves. Anterolateral border usually with four teeth behind exorbital angle; second and third teeth prominent, third tooth in particular most laterally pointed; fourth tooth more or less developed; anterolateral border granular with first tooth connected to exorbital angle by crest, but also with clusters or rows of granules passing ventrally. Front wide, straight or slightly convex, with long submarginal granular crest. Anterior border of the buccal cavity with sharp, sinuous rim, with distinct lateral fissures. Endostomial crests incomplete; lacinie of first maxilliped very short transversely, such that distant from median line, with anterior border incurved, and advanced little in front of prelabial space. Chelipeds very unequal, large claw rather massive and with fingers short; small claw thinner with cutting margins sharp, very elongated, pointed and with tips crossing. Ambulatory legs long and narrow. Sternal plastron with episternites having convex latero-external border. Male abdomen short, broad. Male G1 stocky, incurved and twisted, with spiniform tubercles extending over half length, and with apical bouquet of long and strong incurved setae. (Modified after GUINOT, 1967).

REMARKS

Nanocassiope Guinot (1967) now contains six species: the type of the genus, *N. melanodactylus* (A. Milne Edwards, 1867) from the tropical and subtropical eastern Atlantic; *N. polita* (Rathbun, 1893) from the Pacific coast of America; *N. alcocki* (Rathbun, 1902) from the western Indian Ocean; *N. granulipes* (Sakai, 1939) from Japan and questionably from South Africa; *N. oblonga* sp. nov. from French Polynesia; and *N. tridentata* sp. nov. from Indonesia.

Nanocassiope oblonga sp. nov.
(Fig. 1)

TYPE MATERIAL. — The single male (MNHN-B22782) is the holotype, the three females, paratypes.

MATERIAL EXAMINED. — French Polynesia. SMCB (J. POUPIN): Marquises Islands: Eiao, Stn D74, 7°59.81'S, 140°45.23'W, dredged, 155 m, 19.01.1991: 1 ♂ 4.7 × 3.0 mm, holotype (MNHN-B22782). *Ibidem*: 1 ♀ 4.3 ×

2.7 mm, paratype (MNHN-B22783). *Ibidem*: 1 ♀ 3.8 × 2.4 mm, paratype (QM). Nuku Hiva, Stn D83, 8°47.60'S, 140°05.00'W, dredged, 140 m, 25.01.1991: 1 ovig. ♀ 4.5 × 2.8 mm, paratype (MNHN-B22784).

ETYMOLOGY. — Named in reference to the very wide carapace.

DISTRIBUTION. — Only recorded from French Polynesia. Bathymetric range: 140-155 m.

DESCRIPTION

Carapace transversely ovoid, *c.* 1.57-1.61 times broader than long; conspicuously granular over anterior half, receding posterolaterally; without setae; convex anteriorly, more or less flat from side to side across postero-branchial regions, but depressed near lateral margin. Regions poorly indicated, mostly marked by shallow smooth grooves; 1F and 2F confluent, swollen, coarsely granular; 1M marked anteriorly by row of coarse granules, confluent with inner branch of 2M; 2M broad, divided anteriorly by short groove, outer branch also with raised granular row; anterior prolongation of 3M clearly marked, narrow, posteriorly 3M less clearly marked; 4M not separated; 1L not defined; 2L, 3L, 4L and 5L confluent, with raised granular row anteriorly; 6L not defined; 1R, 2R confluent, with raised anterior granular row; 1P and 2P separated by short, indistinct, cardio-intestinal groove. Anterolateral border of carapace divided into four granular teeth; first tooth clearly separated from exorbital angle, lower than second and third; second slightly larger than third, anteriorly directed; third more laterally directed; fourth tooth very small. Greatest carapace width across third teeth. Posterolateral border markedly convergent, straight or slightly convex, longer than anterolateral. Posterior border costate. Front not produced, divided into two slightly convex lobes by small median notch; laterally clearly separated from supra-orbital angles. Supra-orbital border granular; median and lateral fissures closed, inconspicuous. Infra-orbital border granular, with broad triangular tooth at inner end visible dorsally; deep broad notch below exorbital angle. Eyestalk with 2-3 strong tubercles on edge of cornea, and low tubercle on extension over cornea. Basal antennal segment minutely granular, in contact with ventral prolongation of front; flagellum slightly longer than width of orbit. Basal segment of antennule granular laterally, with moderately strong ridges on superior and lateral margins, flagellum folding obliquely.

Third maxilliped: merus *c.* 0.6 times length of ischium, wider than long, anteroexternal angle moderately produced, bluntly rounded, surface granular; ischium *c.* 1.6 times longer than wide.

Chelipeds noticeably unequal, right largest and stoutest. Merus of right cheliped minutely granular on outer face, upper border coarsely granular, without subterminal or terminal teeth. Carpus rounded, with coarse granular striations, bearing a strong triangular tooth at inner angle. Palm high, height *c.* 0.5 times length (including fixed finger); coarsely granulated, size diminishing ventrally; broad shallow depression before median longitudinal granular crest on upper margin; inner proximal margin with 2-3 larger granular tubercles; immoveable finger relatively long, ventral sub-marginal groove, cutting edge with largest tooth proximo-medially. Dactyl with clearly defined, relatively sharp, longitudinal ridge forming entire superior margin; cutting margin with low teeth increasing in size proximally, and larger, blunt, outwardly and backwardly projecting molar basally. Left cheliped of same form but fingers thinner and cutting margins sharper; dactyl lacking basal molar. Fingers of both chelae tan coloured on one female, not obviously coloured on other specimens.

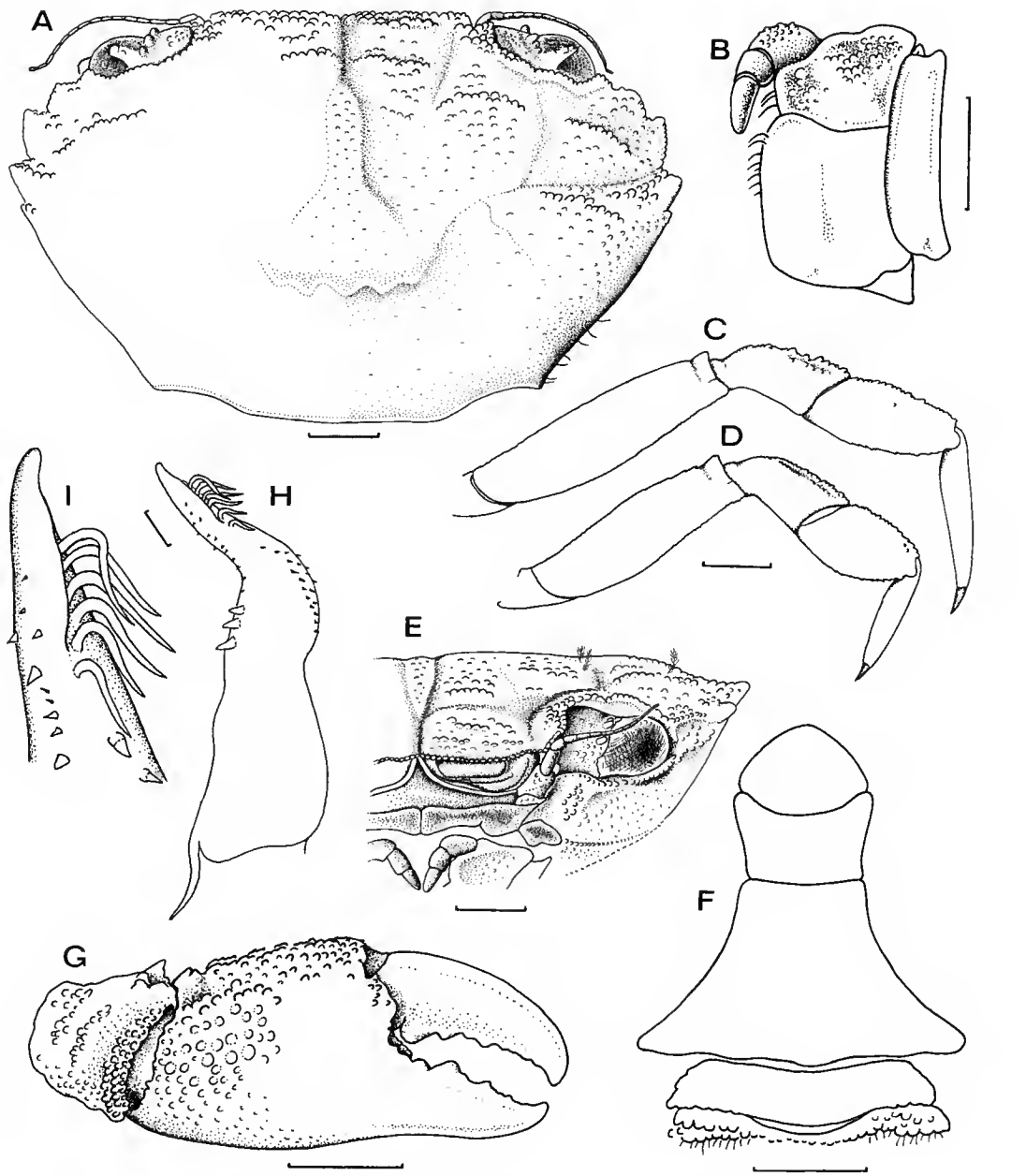

FIG. 1. — *Nanocassiope oblonga* sp. nov., Eiao, Marquises Islands, French Polynesia, holotype, 4.7 × 3.0 mm (MNHN-B22782): A, dorsal carapace; B, third maxilliped; C, third walking leg; D, fourth walking leg; E, frontal view of epistome and infra-orbital margin; F, abdomen; G, right chela; H, I, first gonopod. Scale lines: A-F = 0.5 mm, G = 1 mm, H = 0.1 mm.

Nanocassiope oblonga *sp. nov., Eiao, îles Marquises, Polynésie française, holotype, mâle 4,7 × 3,0 mm (MNHN-B22782) : A, carapace, vue dorsale ; B, troisième maxillipède ; C, troisième patte ambulatoire ; D, quatrième patte ambulatoire ; E, vue frontale de l'épistome et bord infra-orbitaire ; F, abdomen ; G, pince droite ; H, I, premier pléopode. Échelles : A-F = 0,5 mm, H = 0,1 mm.*

Walking legs of medium length, second pair slightly the longest, *c.* 1.1 times carapace width. Margins of meri, carpi, and propodi sharply, and distinctly granulated. Third leg: merus *c.* 3.3 times longer than wide; carpus *c.* 2.3 times longer than wide; propodus 2.5 times longer than wide; dactylus *c.* 1.1 times longer than propodus.

Sternum with groove separating fused sternites 3/4 strongly incised laterally, but not apparent across most of width; long longitudinal fissure on sternite 4. Male abdomen smooth; segment 3-5 fused; telson broadly rounded, *c.* 1.5 times wider than long, deeply sunken into segment 6, subequal in length to lateral border of sixth; sixth segment with lateral margins convergent towards base, *c.* 1.6 times wider than long (measured at widest and longest points); third segment the widest, laterally triangular. G1 as figured; three strong, broad, spines medially on inner margin.

REMARKS

Nanocassiope oblonga sp. nov. is most closely allied to *N. alcocki* (Rathbun, 1902) from which it can be separated by the following characters:

1) the first anterolateral tooth is broader, lower, and less acute;

2) the fourth anterolateral tooth is much reduced and placed on the posterolateral margin, whereas on *N. alcocki* it is prominent, broad, and only a little smaller than the third;

3) the anterolateral margins are generally less granular;

4) the outer face of the major chela is granular over most of its surface, whereas on *N. alcocki* the ventral face is smooth;

5) the shape and pattern of setation on the male G1 is different, especially by *N. oblonga* having a longer, less twisted, apex (*cf.* fig.1H with GUINOT, 1967: fig. 12a,b);

6) it is apparently a smaller species with one female being ovigerous at 4.5 mm c.b., and the largest specimen, the male, being only 4.7 mm across; *N. alcocki* reaches 26 mm across the carapace.

Nanocassiope tridentata sp. nov.
(Fig. 2)

Nanocassiope orientalis Serène, Romimohtarto & Moosa, 1974: 22 (non *Microcassiope orientalis* Takeda and Miyake, 1969: 201).

TYPE MATERIAL. — Holotype is the unique male available for study.

MATERIAL EXAMINED. — Indonesia, Ambon Bay, Rumphius Expedition I: Cruise 3, Stn D19, dredged, bottom of coarse sand and stones, 25.01.1973: 1 ♂ 4.2 × 2.9 mm, holotype (MNHN-B10015).

ETYMOLOGY. — Name refers to the presence of only three obvious anterolateral teeth behind the exorbital angle, which helps to distinguish the species.

DISTRIBUTION. — Only known from the type locality, in the waters near Ambon, Indonesia.

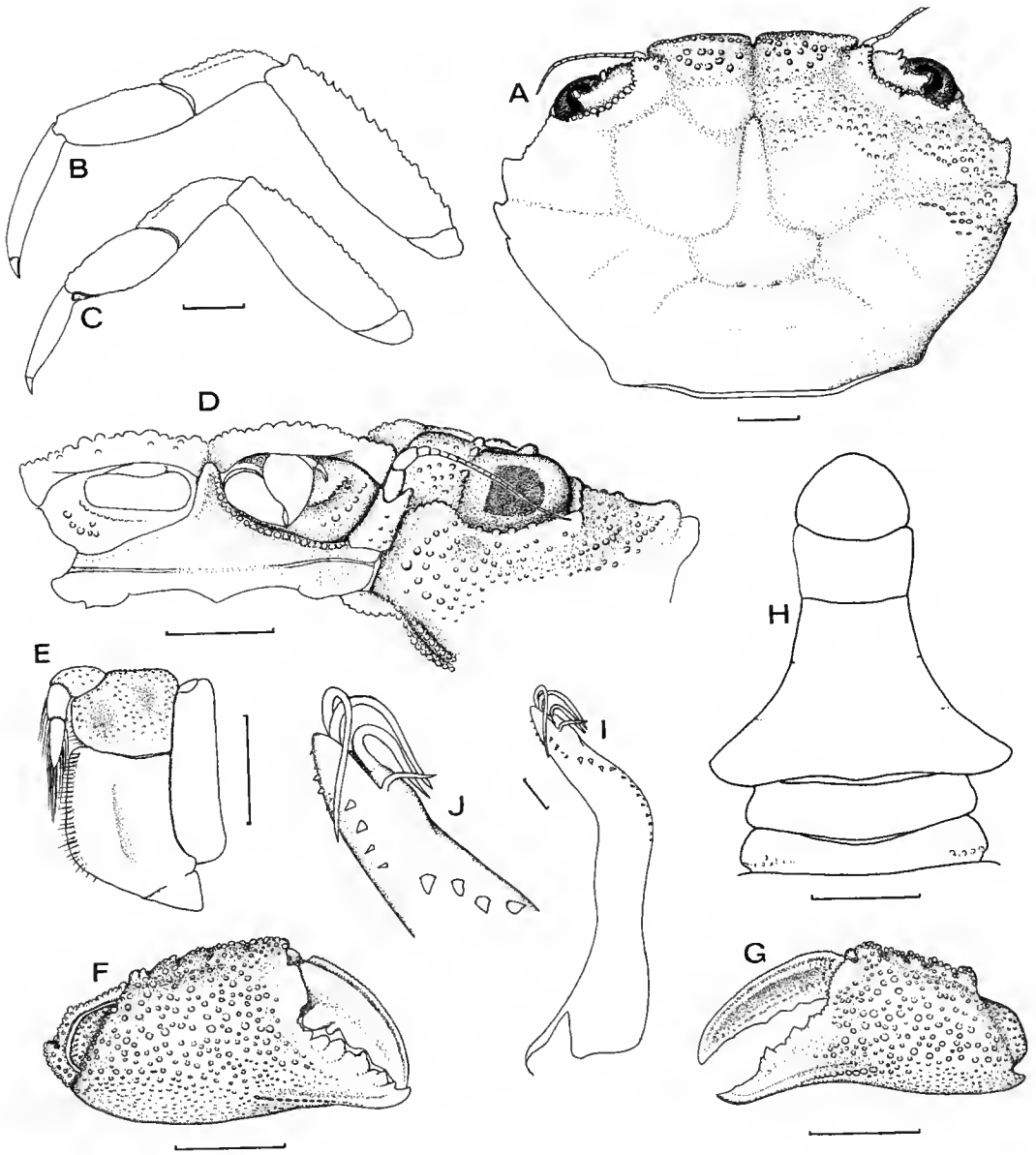

FIG. 2. — *Nanocassiope tridentata* sp. nov. Ambon, Indonesia, holotype – 4.2 × 2.9 mm (MNHN-B10015): A, dorsal carapace; B, third walking leg; C, fourth walking leg; D, frontal view of epistome and infra-orbital margin; E, third maxilliped; F, right chela; G, left chela; H, male abdomen; I, J, first gonopod. Scale lines: A-E, F = 0.5 mm; F, G = 1 mm; H = 0.1 mm.

Nanocassiope tridentata *sp. nov., Ambon, Indonésie, holotype, mâle, 4,2 mm × 2,9 mm (MNHN-B10015) : A, carapace, vue dorsale ; B, troisième patte ambulatoire ; C, quatrième patte ambulatoire ; D, troisième maxillipède ; E, vue frontale de l'épistome et bord infra-orbitaire ; F, abdomen ; G, pince droite ; H, I, premier pléopode. Échelles : A-E = 0,5 mm, F, G = 1 mm, H = 0,1 mm.*

DESCRIPTION

Carapace *c.* 1.45 times broader than long; conspicuously granular over anterior half, receding posterolaterally; without marked setation; convex anteriorly, more or less flat from side to side across postero-branchial regions. Regions relatively well marked by smooth grooves; 1F and 2F confluent, swollen, coarsely granular; 1M poorly but completely defined; 2M broad, undivided; anterior prolongation of 3M clearly marked, narrow, posteriorly 3M less clearly marked; 4M not separated; 1L not defined; 2L and 3L confluent; 4L and 5L shallowly separated; indistinct, cardio-intestinal groove. Anterolateral border of carapace divided into three granular teeth; first tooth largest, broad, triangular, broadly separated from exorbital angle; second slightly smaller and narrower; third tooth very small. Greatest carapace width across third teeth. Posterolateral border markedly convergent, straight or slightly convex, longer than anterolateral. Posterior border costate. Front not produced, divided into two slightly convex lobes by small median notch; laterally clearly separated from supra-orbital angles. Supra-orbital border granular; median and lateral fissures small but distinct. Infra-orbital border granular, with broad, blunt, triangular tooth at inner end; deep broad notch below exorbital angle. Eyestalk with 2-3 strong tubercles on edge of cornea, and further tubercle on extension over cornea. Basal antennal segment minutely granular, barely in contact with ventral prolongation of front; flagellum about as long as width of orbit. Basal segment of antennule granular laterally, flagellum folding slightly obliquely. Anterior margins of epistome granular.

Third maxilliped: merus *c.* 0.6 times length of ischium, wider than long, anteroexternal angle slightly produced, rounded, surface granular; ischium *c.* 1.3 times longer than wide.

Chelipeds noticeably unequal, right largest and stoutest. Merus of right cheliped granular on outer face, upper border with row of large pointed tubercles separated from broad blunt terminal lobe. Carpus with coarse granular elevations, bearing strong triangular granular tooth at inner angle. Palm high, height *c.* 0.5 times length (including fixed finger); coarsely granulated, size diminishing ventrally; broad shallow depression on upper outer margin before dorsal surface; inner proximal margin with row of larger rounded granules; immoveable finger relatively long, ventral submarginal groove, cutting edge with large teeth. Dactyl with clearly defined, relatively sharp, granulated longitudinal ridge along entire superior margin; cutting margin with low teeth increasing in size proximally, and larger, blunt, outwardly and backwardly projecting molar basally. Left cheliped of same form but fingers thinner and cutting margins sharper; dactyl lacking basal molar. Fingers of both chelae without trace of colouring in preserved specimen.

Walking legs of medium length, third pair *c.* 1.1 times carapace width. Anterior margins of meri and carpi coarsely granulated, forming two broad lobes on each segment. Third leg: merus *c.* 3.3 times longer than wide; carpus *c.* 2.3 times longer than wide; propodus *c.* 2.2 times longer than wide; dactylus *c.* 1.1 times longer than propodus.

Sternum with groove separating fused sternites 3/4 incised laterally, but only broad shallow groove across most of width; long longitudinal fissure on sternite 4. Male abdomen smooth; segment 3-5 fused; telson broadly rounded, *c.* 1.3 times wider than long, moderately sunken into segment 6, *c.* 1.2 times length of lateral border of sixth; sixth segment with lateral margins slightly convergent towards base, *c.* 1.6 times wider than long (measured at widest and longest points); third segment the widest, laterally triangular. G1 relatively narrow; four subapical reflexed stout setae; otherwise as figured.

REMARKS

This specimen was found in the collection of the MNHN with the label carrying the questioned name "*Nanocassiope ? orientalis ?*", with the identifier also questioned as SERÈNE. Indeed, SERÈNE *et al.* (1974) did list this species in the list of identifications of the collection made by the Rumphius Expedition I. On close scrutiny however it is apparent that this preliminary identification is not correct because there are many differences between the two taxa. Most importantly TAKEDA and MIYAKE (1969) described their species in the genus *Microcassiope* Guinot, 1967, and there is no reason to doubt this placement. *Microcassiope orientalis* certainly does not belong to *Nanocassiope*, as it is presently defined, because it lacks the long, stiff, recurved bristles on the male G1 which are so characteristic of all the species of that genus.

Nanocassiope tridentata sp. nov. is most closely related to *N. granulipes* (Sakai, 1939). It differs from that species, and all the other described species, by having only three anterolateral teeth behind the exorbital angle instead of four, the first being vestigial and represented by only one or two slightly raised granules. *N. tridentata* further differs from *N. granulipes* by having the entire outer face of the cheliped palm covered in coarse granules; in the later species the palm is "dorsally slightly carinate and granulated but its external surface near the inferior border is smooth" (SAKAI, 1939: 547). The anterior extension of 3M is narrow, while on *N. granulipes* it is relatively wide and more obviously tapering (cf. SAKAI, 1939: fig. 59). Finally, the male G1 is narrower and less stout than the other described species.

Acknowledgments

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Une espèce nouvelle de *Neocallichirus* aux îles Tuamotu, Polynésie française (Crustacea, Decapoda, Thalassinidea)

par Nguyen NGOC-HO

Résumé. — Une espèce nouvelle de la famille des Callianassidae récoltée en Polynésie française, *Neocallichirus taiaro*, est décrite et illustrée. Elle est proche d'un groupe d'espèces dont l'endopodite des uropodes est plus large que long et surtout de *Neocallichirus lemaitrei* Manning provenant de Colombie, à laquelle elle est comparée.

Mots-clés. — Crustacea, Decapoda, Thalassinidea, Callianassidae, taxonomie, *Neocallichirus*, espèce nouvelle, Polynésie française.

A new species of *Neocallichirus* from the Tuamotu Islands, French Polynesia (Crustacea, Decapoda, Thalassinidea)

Abstract. — A new species of the Callianassidae from French Polynesia, *Neocallichirus taiaro*, is described and figured. It is related to a group of species whose uropodal endopod is broader than long, and especially to *Neocallichirus lemaitrei* Manning from Colombia. Distinguishing characters between the two species are discussed.

Keyword. — Crustacea, Decapoda, Thalassinidea, Callianassidae, taxonomy, *Neocallichirus*, new species, French Polynesia.

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INTRODUCTION

Dans le matériel de crustacés Décapodes récolté par Joseph POUPIN lors de son voyage en Polynésie française, en février 1994, se trouve un spécimen femelle de Callianassidae appartenant à une espèce encore non décrite du genre *Neocallichirus* Sakai. Elle est présentée ici comme une espèce nouvelle, *Neocallichirus taiaro*.

Le genre *Neocallichirus* a été établi en 1988 par SAKAI qui y inclut les espèces australiennes *N. horneri* Sakai 1988, espèce-type, *N. darwinensis* Sakai 1988, *N. limosa* (Poore, 1975), *N. caechabitator* Sakai, 1988, ainsi que les espèces américaines *N. grandimana* (Gibbes, 1850) et *N. rathbunae* (Schmitt, 1935), les espèces indonésiennes *N. indica* (de Man, 1905) et *N. moluccensis* (de Man, 1905), l'espèce sud-africaine *N. natalensis* (Barnard, 1947) et l'espèce est-atlantique *N. sassendrensis* (Le Lœuff & Intès, 1974).

À cette liste, MANNING & FELDER (1991) ajoutaient quatre espèces américaines ouest-atlantiques *N. guara* (Rodrigues, 1971), *N. guassutinga* (Rodrigues, 1971), *N. mirim* (Rodrigues,

1971) et *N. trilobata* (Biffar, 1970). Ces espèces seront ultérieurement séparées par MANNING & LEMAÎTRE (1993) en un genre nouveau *Sergio*. En 1993, MANNING signalait deux nouvelles espèces de *Neocallichirus* en provenance de la mer des Caraïbes, *N. nickellae* et *N. lemaitrei*. La première espèce de ce genre dans l'océan Indien a été décrite par KAZMI & KAZMI (1992), et NGOC-HO (1994) décrit une autre espèce nouvelle d'Australie, *N. denticulatus*. *N. taiaro,* qui fait l'objet de cette note, est la première espèce de *Neocallichirus* signalée en Polynésie française.

Les dimensions indiquées se rapportent à la longueur de la carapace (l.c.), mesurée de l'extrémité du rostre au bord postérieur de la carapace et à la longueur totale (l.t.), mesurée de l'extrémité du rostre au bord postérieur du telson.

Genre **NEOCALLICHIRUS** Sakai, 1988

Neocallichirus taiaro sp. nov.
(Fig. 1-2)

HOLOTYPE. — Polynésie française : îles Tuamotu, atoll de Taiaro ; 15°45' S-144°40' W ; J. POUPIN coll., à la main dans terrier de sable fin corallien, 12-14 février 1994 / SMCB : ♀, l.c. 8,5 mm, l. t. 32 mm (MNHN-Th 1291).

ÉTYMOLOGIE. — L'espèce est nommée d'après sa localité-type.

DESCRIPTION

Carapace (fig. 1a, 1b) avec ovale céphalo-thoracique bien délimité, sillon cervical profond, placé au 4/5^{e} environ de la longueur de la carapace ; *linea thalassinica* distincte. Rostre largement triangulaire, à sommet obtus, dépassant à peine la base des pédoncules oculaires ; saillies latérales, de part et d'autre des pédoncules oculaires, très faibles.

Pédoncules oculaires comprimés dorso-ventralement, à extrémité obtuse, atteignant la base du 2^{e} segment des antennules et portant vers le milieu des cornées latéro-dorsales globuleuses.

Pédoncules antennulaires plus courts que les pédoncules antennaires (fig. 1b), munis de longues soies, avant-dernier segment plus court que le dernier ; longues soies denses sur les flagelles.

Pédoncules antennaires munis de quelques longues soies, dépassant ceux des antennules de la moitié du dernier segment, avant-dernier segment plus long que le dernier, écaille antennaire en petit lobe ; flagelles avec peu de soies.

Premiers maxillipèdes (fig. 1d) avec épipodite pourvu d'un lobe antérieur bien développé, à sommet aigu ; endopodite rudimentaire, en un petit lobe arrondi.

Deuxièmes maxillipèdes (fig. 1e) munis d'un petit épipodite ; exopodite d'aspect foliacé.

Troisièmes maxillipèdes (fig. 1f, 1g) sans exopodite, ni épipodite ; ischion et mérus subpédiformes, une rangée oblique d'épines à la face mésiale de l'ischion ; propode dilaté ventralement, plus de quatre fois plus large que le dactyle ; dactyle effilé, environ quatre fois plus long que large.

Grand péréiopode 1 (fig. 2a) à droite, puissant ; ischion et mérus à peu près de même longueur, ischion deux fois moins large, faiblement denté ventralement, mérus avec lobe ventral saillant portant une douzaine d'épines ; carpe plus court que le mérus, à peu près aussi large

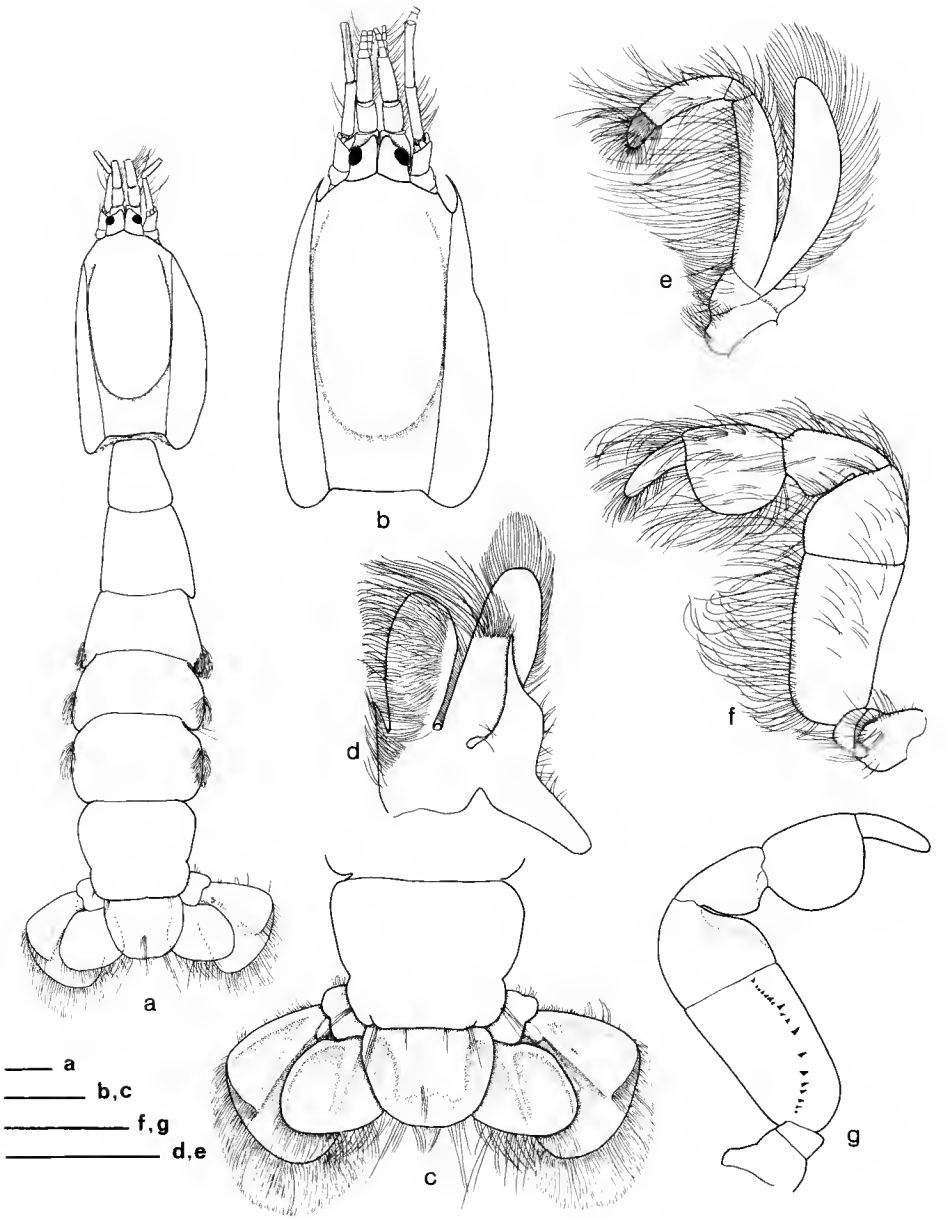

FIG. 1. — *Neocallichirus taiaro* sp. nov., holotype : a, animal entier, vue dorsale ; b, céphalothorax, vue dorsale ; c, telson et uropodes, vue dorsale ; d, e, f, 1er, 2^{e} et 3^{e} maxillipède respectivement, vue ventrale ; g, 3^{e} maxillipède, dénudé, vue mésiale. Échelle : 2 mm.

Neocallichirus taiaro *sp. nov., holotype: a, body in dorsal view; b, cephalothorax in dorsal view; c, telson and uropod in dorsal view; d, e, f, maxilliped 1, 2 and 3 respectively in ventral view; g, maxilliped 3, setae omitted, in mesial view. Scale bar: 2 mm.*

que la portion palmaire de la main, muni de 3 épines ventrales distales ; paume environ 2,5 fois plus longue que le carpe, portant 13 petites épines distribuées du 1/4 au 2/3 du bord ventral ; doigt fixe aussi long que le dactyle, avec 5 tubercules (un grand, quatre petits) à sommet arrondi dans la région proximale du bord préhensile et une rangée de 3 autres tubercules proximaux, visibles sur le côté externe ; dactyle à extrémité légèrement incurvée, bord préhensile avec 2 petites dents vers son milieu.

Petit péréiopode 1 (fig. 1b) plus grêle, ischion avec une dizaine de denticules ventraux, à peu près aussi long que le mérus ; carpe 0,8 fois aussi long que le mérus et presque 2 fois plus large ; paume légèrement plus longue que le carpe ; doigt fixe et dactyle de même longueur et de même longueur que le carpe.

Péréiopodes 3 (fig. 2d) à propode dilaté ventralement mais ne dépassant pas le bord ventral du carpe.

Péréiopodes 4 (fig. 2e) avec une saillie disto-ventrale au propode leur conférant un aspect subchéliforme.

Péréiopodes 5 (fig. 2f) à extrémité subchéliforme.

Abdomen (fig. 1a) dont le dernier segment est le plus long ; rapports approximatifs de longueur des autres segments par rapport à celui-ci (= 1) : 5^{e} et 2^{e} = 0,85 ; 4^{e} et 3^{e} = 0,65 ; 1^{er} = 0,75.

Pléopodes 1 (fig. 2g) biarticulés, grêles.

Pléopodes 2 (fig. 2h) munis d'un exopodite, un *appendice interna* placé au quart distal environ du bord latéral interne de l'endopodite.

Pléopodes 3-5 (fig. 2i) à exopodite et endopodite larges, un petit *appendice interna* encastré à peu près au milieu du bord interne de l'endopodite.

Telson (fig. 1c) légèrement plus large dans sa partie proximale que long, bord postérieur faiblement arrondi.

Uropodes (fig. 1c) : exopodite à bord postérieur légèrement convexe, lobe antéro-dorsal occupant presque la moitié de l'article, et s'écartant peu du bord distal ; endopodite plus large que long, à bord postérieur presque rectiligne.

Remarques

Le nouveau taxon présente les caractères de *Neocallichirus* signalés dans la diagnose du genre par Sakai (1988), puis Manning & Felder (1991), à l'exception de ses cornées qui sont dorso-latérales et globuleuses au lieu d'être dorsales et aplaties (*dorsal, disk-shaped*). Des cornées semblables à celles de *N. taiaro* ont déjà été décrites chez certaines espèces ouest-atlantiques, notamment chez *N. grandimana* (Gibbes), *N. rathbunae* (Schmitt), *N. nickellae* Manning et aussi chez *N. manningi* (Kazmi & Kazmi) de Karachi. D'après Manning (1993), les trois espèces ouest-atlantiques de *Neocallichirus* constituent, avec *N. lemaitrei* Manning de Colombie et *N. horneri* Sakai d'Australie, un groupe d'espèces qui ont un endopodite des uropodes plus large que long, aplati distalement, et un bord postérieur du telson arrondi ou faiblement concave. *N. taiaro* est proche de ce groupe et en particulier de *N. lemaitrei* à laquelle elle ressemble aussi par les caractères suivants :

1) rostre et projections frontales de la carapace très faibles ;

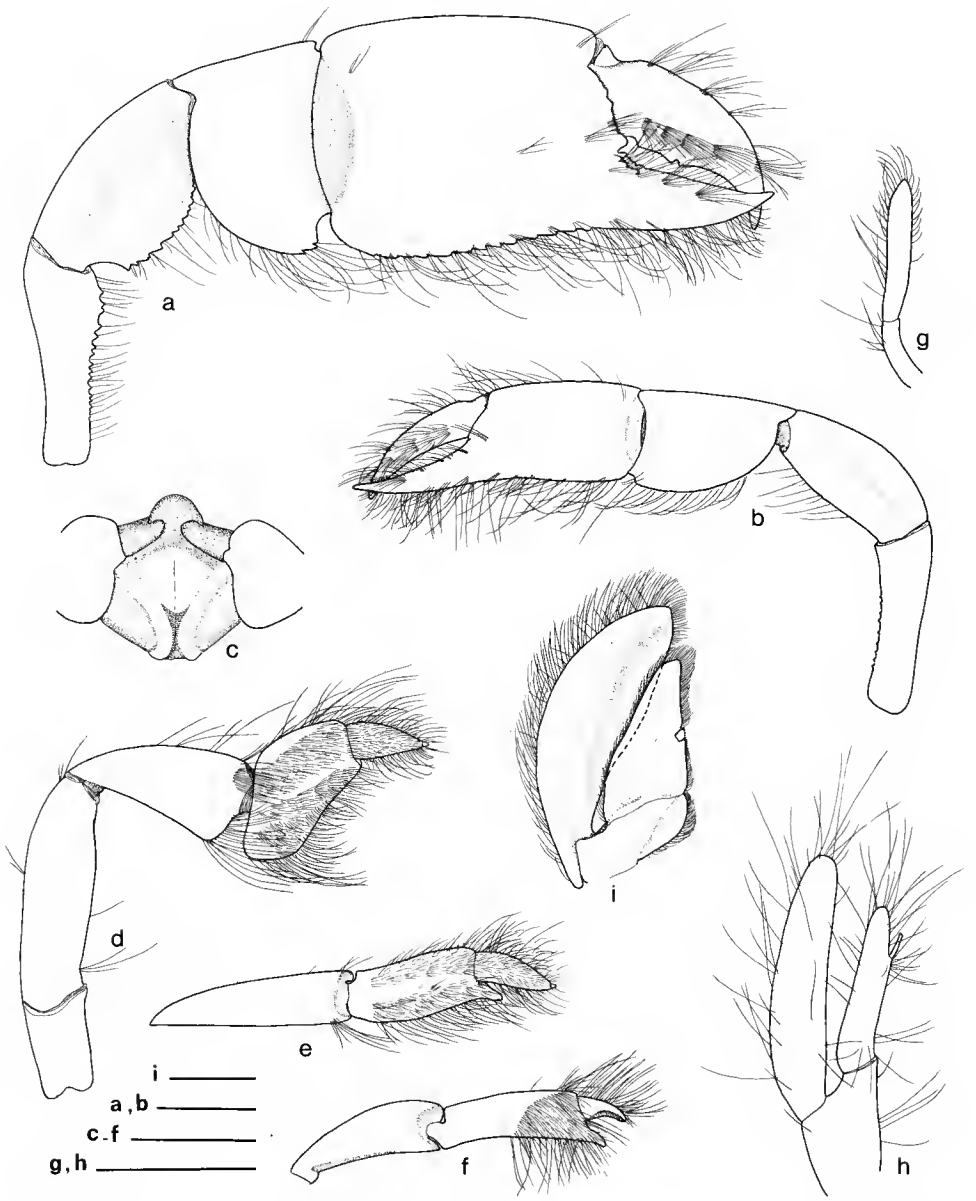

FIG. 2. — *Neocallichirus taiaro* sp. nov., holotype : a, grand péréiopode 1 ; b, petit péréiopode 1 ; c, 3e sternite, vue ventrale ; d, péréiopode 3 ; e, f, partie distale du péréiopode 4 et 5 respectivement ; g, pléopode 1 ; h, pléopode 2 ; i, pléopode 3. Échelle : 2 mm.

Neocallichirus taiaro *sp. nov., holotype: a, large pereopod 1; b, small pereopod 1; c, 3rd sternite in ventral view; d, pereopod 3; e, f, distal part of pereopod 4 and 5 respectively; g, pleopod 1; h, pleopod 2; i, pleopod 3. Scale bar: 2 mm.*

2) telson légèrement plus large que long ;

3) morphologie et spinulation du grand péréiopode 1 de la femelle ;

4) morphologie et spinulation des péréiopodes 3-5 ;

Les deux espèces peuvent être différenciées de la façon suivante :

1) cornées globuleuses chez *N. taiaro*, aplaties chez *N. lemaitrei* (voir MANNING, 1993 : fig.1a, 1b, 1c) ;

2) propode du maxillipède 3 régulièrement arrondi et lisse au bord ventro-distal chez *N. taiaro*, légèrement denticulé à ce bord chez *N. lemaitrei* ;

3) proportions différentes du petit péréiopode 1 de la femelle, en particulier le carpe est plus court que la paume chez *N. taiaro*, plus long chez *N. lemaitrei* ;

4) exopodite des uropodes approximativement aussi long que sa largeur au bord distal et le lobe dorsal occupant moins de la moitié de l'appendice chez *N. taiaro* ; exopodite des uropodes environ 1,5 fois plus large que long et le lobe dorsal occupant à peu près la moitié de l'article chez *N. lemaitrei*.

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